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Life and Earth Sciences

NO. 9

Assembling a Taxonomic Monograph of Tribe Wirthiotremateae (Lichenized Ascomycota: Ostropales: Graphidaceae)

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April 28, 2017
Publication 1569

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

FIELDIANA

Publication Note

Fieldiana: *Life and Earth Sciences*, ISSN 2158-5520
Formed by the merger of:
Fieldiana: *Botany* (ISSN 0015-0746);
Fieldiana: *Geology* (ISSN 0096-2651);
Fieldiana: *Zoology* (ISSN 0015-0754).

Mission

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Cover: Asteristion platycarpum (photo: R. Lücking)

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Life and Earth Sciences

NO. 11

Sperm Ultrastructure of the Protobranchia: Comparison with Other Bivalve Mollusks and Potential Taxonomic and Phylogenetic Significance

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Received October 19, 2016
Accepted October 19, 2016
Published April 28, 2017
Publication 1569

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

©2017 Field Museum of Natural History
ISSN 2158-5520
PRINTED IN THE UNITED STATES OF AMERICA

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Assembling a Taxonomic Monograph of Tribe Wirthiotremateae (Lichenized Ascomycota: Ostropales: Graphidaceae)

Ian D. Medeiros, Ekaphan Kraichak, Robert Lücking, Armin Mangold, and H. Thorsten Lumbsch

Abstract

Phylogenetic studies of the lichenized fungal family Graphidaceae necessitate various nomenclatural changes. Tribe Wirthiotremateae is more narrowly circumscribed on the basis of new molecular data and phenotypical differences towards allied clades. The new genus *Austrotrema* is described to accommodate the three species of the *Thelotrema bicinctulum* group, *Asteristion* is resurrected for the seven species of the *Chapsa platycarpa* group, and *Nadvornikia* is expanded to include two non-mazaediate species in addition to its two mazaediate species. *Asteristion australianum* is newly described for Australian material previously identified as *T. albo-olivaceum*. Eleven new combinations are made: *Asteristion alboannuliforme* (Bas.: *Thelotrema alboannuliforme*), *As. albo-olivaceum* (Bas.: *T. albo-olivaceum*), *As. cupulare* (Bas.: *T. cupulare*), *As. leucophthalmum* (Bas.: *T. leucophthalmum*), *As. platycarpoides* (Bas.: *T. platycarpoides*), *As. platycarpum* (Bas.: *T. platycarpum*), *Austrotrema bicinctulum* (Bas.: *T. bicinctulum*), *Au. myriocarpum* (Bas.: *T. myriocarpum*), *Au. terebrans* (Bas.: *T. terebrans*), *Nadvornikia expallescens* (Bas.: *Leucodecton expallescens*), and *N. peninsulae* (Bas.: *Myriotrema peninsulae*). Descriptions and discussions of Wirthiotremateae species are provided, along with keys to the species of the tribe. Phylogenetic analyses were based on six markers: the mitochondrial small subunit (mtSSU) and nuclear large subunit (nuLSU) rDNA, RNA polymerase II largest (RPB1) and second largest (RPB2) subunit, elongation factor 1 alpha (EF1-α), and internal transcribed spacer (ITS).

Key Words: lichen systematics, tropical lichens, thelotremoid Graphidaceae, identification key, Cuba, Puerto Rico, Thailand, Philippines, Australia, Fiji

Introduction

In recent years, molecular data have shown that the lichenized fungal family Graphidaceae, traditionally characterized by elongate, script-like ascomata (lirellae), includes the formerly independent family Thelotremataceae, with rounded ascomata, and possibly also (as subfamily Gomphilloideae) the families Gomphillaceae, Asterothyriaceae, and Solorinellaceae (Mangold et al., 2008; Baloch et al., 2010; Rivas Plata et al., 2012b, 2013). In its current circumscription, Graphidaceae is by far the most species-rich family of crustose tropical lichenized fungi (Staiger, 2002; Frisch et al., 2006a; Lücking, 2008; Rivas Plata et al., 2012a,b, 2013). Some 2500 species are presently known, which means that more than 25% of the known diversity of lichenized fungi is concentrated in the two hyperdiverse families Graphidaceae and Parmeliaceae (Lücking et al., 2014; Kraichak et al., 2015a). In addition, quantitative predictions suggest that another 1800 species of Graphidaceae have yet to be discovered and described (Lücking, 2012; Lücking et al., 2014).

The majority of species in Graphidaceae forms crusts on tree bark, although the family also contains saxicolous, foliicolous, muscicolous, and lignicolous taxa. Corticolous crustose lichens provide a microhabitat for a number of often host-specific, lichenicolous fungi as well as food for invertebrates such as gastropods and psocids (Gerson, 1973; Lücking & Bernecker-Lücking, 2000; Lawrey & Diederich, 2015). Lichen communities in tropical rain forests are dominated by species in the families Graphidaceae, Pyrenulaceae, and Trypetheliaceae (Aptroot, 2012; Nelsen et al., 2014), and these communities are a significant source of algal and fungal diversity (Lücking et al., 2009a,b; Nelsen et al., 2011). Species with more or less rounded ascomata, formerly separated in the family Thelotremataceae and now commonly labeled "thelotremoid Graphidaceae," have been identified as effective bioindicators of ecological continuity in tropical forests (Rivas Plata et al., 2008; Weerakoon et al., 2010).

The genera corresponding to the former family Thelotremataceae were historically separated by features of the ascospores (Müller, 1887a) or the excipulum (Salisbury, 1978; Hale, 1980). More recent generic concepts have relied on a larger number of characters (Frisch, 2006; Frisch & Kalb, 2006; Rivas Plata et al., 2010a), together with molecular data working continuously towards a more natural generic concept (Rivas Plata et al., 2012b, 2013). Nevertheless, the large genera *Thelotrema* Ach. and *Myriotrema* Fée, and even some of the recently segregated or reinstated genera, such as *Leucodecton* A. Massal., remain polyphyletic. This study attempts to remedy some of these issues, focusing on the *Wirthiotrema* clade, which was delimited by Rivas Plata et al. (2013) and then formally included in the newly described tribe Wirthiotremateae by Lumbsch et al. (2014a). The core group of this clade, the *Thelotrema glaucopallens* group, was initially characterized as a group distinct from *Thelotrema* s.s. or *Myriotrema* s.s. by Frisch (2006); Rivas Plata and Lumbsch (2011) subsequently showed with molecular evidence that other lineages also belong in the vicinity of this group.

As defined here, tribe Wirthiotremateae includes the *Chapsa platycarpa* group, for which the genus *Asteristion* Leight. is resurrected, containing species previously placed in *Thelotrema*, *Ocellularia* G. Mey., *Chapsa* A. Massal., and *Phaeotrema* Müll. Arg.; the *Thelotrema bicinctulum* group, for which the genus *Austrotrema* I. Medeiros, Lücking & Lumbsch is newly described, containing species previously treated in

Thelotrema; the genus *Nadvornikia* Tibell, traditionally comprising two mazaediate species but expanded here to include two additional, non-mazaediate species previously classified in *Leucodecton* and *Myriotrema*; and the *Thelotrema glaucopallens* group, corresponding to the genus *Wirthiotrema* Rivas Plata, Kalb, Frisch & Lumbsch, containing species previously placed in *Thelotrema*, *Myriotrema*, *Leptotrema* Mont. & Bosch, and *Anthracothecium* Hampe ex A. Massal. All taxa in this group were classified in Thelotremataceae prior to the work of Mangold et al. (2008).

Our objectives in this paper are: (1) to present a revised phylogeny of Wirthiotremateae based on six molecular markers (previous analyses included only three) to delimit the tribe and further elucidate its relationships within Graphidaceae; and (2) to present a monographic revision of the tribe, including descriptions of all Wirthiotremateae taxa with accounts of their distribution and ecology and keys to included taxa and superficially similar species.

Material and Methods

Morphological, Anatomical, and Chemical Studies

Specimens were examined with LEICA MS5, MOTIC K400, and OLYMPUS SZX12 dissecting microscopes and photographed with NIKON Coolpix 5400, SONY Cybershot G, and a JENOPTIC ProgRes C5 microscope digital cameras. Sections of apothecia were cut by hand with a single-edged razor blade and mounted in tap water for examination with ZEISS Axioscop 2, OLYMPUS BH-2, and VISTA VISION VWR V036 compound microscopes, in part connected to a JENOPTIC ProgRes C3 digital microscope camera.

Secondary chemistry was assessed with standard methods of thin-layer chromatography using solvent system C (Culberson, 1972; Orange et al., 2010). KOH solution was flushed through slides with apothecia and thallus sections to routinely check for the presence of the stictic and norstictic acid chemosyndromes. Lugol's iodine solution was flushed through slides with apothecia sections to evaluate amyloidity of ascospores. A few species in Wirthiotremateae (or their look-alikes) possess lichexanthone, which was identified by its yellow florescence in long-wave ultraviolet (UV) light.

Molecular Phylogenetic Studies

New DNA sequences were generated for 16 samples from either new extractions or existing DNA extracts used for previous work. New samples were prepared for extraction by excising apothecia with sterile forceps; when necessary, secondary metabolites were removed prior to extraction with acetone and the material was transferred to a clean tube. DNA was isolated with the SIGMA REDExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, USA), following the manufacturer's instructions. A 1:9 dilution of the DNA extract and nuclease-free water was prepared for each sample and used in most polymerase chain reactions (PCR); for samples that failed to give amplification under standard conditions, more concentrated DNA solutions were used, up to undiluted DNA extracts.

Regions of the following fungal markers were amplified with PCR using published primers and specific thermal cycler programs (Table 1): the mitochondrial small subunit rDNA (mtSSU), the nuclear large subunit rDNA (nuLSU), the RNA polymerase II largest subunit (RPB1) and second largest subunit (RPB2), the elongation factor 1 alpha (EF1-α), and the internal transcribed spacer (ITS) as the fungal barcoding marker. We also attempted to generate sequences for the nuclear gene *Mcm7* (Schmitt et al., 2009), but only succeeded in obtaining two sequences, both from outside the group of interest. PCR reactions were either 10 μL, consisting of 4.5 μL nuclease-free water, 0.5 μL each of the forward and reverse primers, 2.5 μL MyTaq™ Red Mix (Bioline, Taunton, Massachusetts, USA), and 2 μL DNA solution, or 25 μL, consisting of 19 μL nuclease free water, 2.5 μL each of the forward and reverse primers, one Illustra™ PuReTaq™ Ready-to-Go™ PCR bead (GE Healthcare, Buckinghamshire, UK), and 1 (up to 2.5) μL DNA solution. Previous DNA extracts used in this study were several years old (in some cases DNA was amplified from storage tubes from which "all" of the DNA solution had been removed), so the more sensitive 25-μL reactions were generally used. PCR products were run through 1% agarose gels stained with ethidium bromide and visualized under UV light. To clean the PCR products, bands of the anticipated fragment size were cut out of the gel, heated at 70°C for 10 min, and cooled to 45°C for 5 min before 1 μL of GELase (agarose) enzyme (Epicentre Biotechnologies, Madison, Wisconsin, USA) was added. Samples were then incubated at 45°C for at least 24 hours before sequencing.

Each cycle sequencing reaction contained 3.5 μL buffer (a solution of 200 mM Tris and 5 mM $MgCl_2$), 0.6 μL forward or reverse primer, 4.4 μL nuclease-free water, 0.5 μL BigDye® version 3.1 (Applied Biosystems, Foster City, California, USA), and 1 μL cleaned PCR product. Up to 2 μL PCR product was used for samples from which it proved difficult to generate good sequences. Cycle sequencing conditions were: 96°C for 1 min, then 25 cycles of 96°C for 10 s, 50°C for 5 s, and 60°C for 4 min. Samples were precipitated in 30 μL of a 1:12 Ethylenediaminetetraacetic acid (EDTA)–ethanol solution, centrifuged at 4°C until all alcohol had evaporated, rehydrated with 70% ethanol, centrifuged again at 4°C, incubated at 65°C for 10 min, and finally suspended in 10 μL Hi-Di formamide (Life Technologies, Grand Island, New York, USA). Sequencing was carried out via capillary electrophoresis in an Applied Biosystems 3730 DNA Analyzer (Foster City, California, USA). Sequences were assembled in Geneious 5.6.7 or 7.1.5 (Drummond et al., 2012). All newly generated sequences were submitted to GenBank (Table 2).

Sequences were assembled and aligned separately per marker in Geneious using MAFFT, together with select sequences from GenBank (Table 2). Alignments were manually inspected and corrected where necessary. Hypervariable regions, particularly in the ITS, were trimmed out after subjecting the alignments to HoT score analysis (Landan and Graur, 2008; Penn et al., 2010b) on the Guidance web server (http://guidance.tau.ac.il/ver2/; Penn et al., 2010a). Final alignments were subjected to maximum likelihood analysis for each marker using RAxML (Stamatakis, 2014) via the CIPRES Science Gateway (Miller et al., 2010). For each data set, the GTR-Gamma model was applied and the protein-coding markers (RPB1, RPB2, and EF1-α) were further partitioned by codon position. The individual trees were examined for conflicts, and individual sequences causing anomalous placements were removed. A concatenated alignment of all six loci was then analyzed using the same model specifications as outlined above.

TABLE 1. Primers used for PCR and sequencing reactions, with thermal cycler programs specified. The letters F and R after literature citations refer to forward and reverse primer sequences. All primers were made by Integrated DNA Technologies, Inc, Coralville, Iowa, USA. Programs used were (1) Initial denaturation at 95°C for 3 min, followed by 35 cycles of 95°C for 1 min, 51°C for 1 min, then 72°C for 1 min 50 s, concluding with a final elongation at 72°C for 10 min. (2) Initial denaturation at 94°C for 10 min, followed by 35 cycles of 95°C for 45 s, 50°C for 45 s, then 72°C for 1 min 30 s, concluding with a final elongation at 72°C for 10 min. (3) Initial denaturation at 94°C for 1 min 15 s, followed by 35 cycles of 95°C for 35 s, 55°C for 55 s, then 72°C for 42 s. (4) Initial denaturation at 94°C for 4 min, followed by 35 cycles of 94°C for 45 s, 52°C for 45 s, then 72°C for 1 min 30 s, concluding with a final elongation at 72°C for 10 min. (5) Initial denaturation at 94°C for 10 min, followed by 35 cycles of 94°C for 45 s, 50°C for 50 s, then 72°C for 1 min, concluding with a final elongation at 72°C for 5 min. (6) Initial denaturation at 94°C for 3 min, followed by 35 cycles of 94°C for 45 s, 52°C for 1 min, then 72°C for 1 min 30 s, concluding with a final elongation at 72°C for 7 min. (7) Initial denaturation at 94°C for 5 min, followed by 11 cycles of 94°C for 30 s, 60°C (decreasing by 1°C for each subsequent cycle) for 45 s, then 72°C for 30 s, then 20 cycles of 94°C for 30 s, 55°C for 45 s, and 72°C for 30 s, concluding with a final elongation at 72°C for 5 min. (8) Initial denaturation at 94°C for 5 min, followed by 40 cycles of 94°C for 30 s, 48°C for 30 s, then 72°C for 1 min 30 s, concluding with a final elongation at 72°C for 5 min.

Marker	Forward primer	Reverse primer	Source	Program
mtSSU	mrSSU1	mrSSU3R	Zoller et al., 1999 (F, R)	1
mtSSU	MSU1	MSU7	Zhou & Stanosz, 2001 (F, R)	2
nuLSU	AL2R	LR3	Mangold et al., 2008 (F) Vilgalys & Hester, 1990 (R)	3
nuLSU	AL2R	LR6	Mangold et al., 2008 (F) Vilgalys & Hester, 1990 (R)	4
RPB1	RPB1-aF	RPB1-cR	Stiller & Hall, 1997 (F) Matheny et al., 2002 (R)	5
RPB2	GD1-RPB2-7cF	GD-RPB2-11aR	Kraichak et al., 2015b (F, R)	6
EF1-α	Efdf	EF1-1567R	Rehner, 2001 (F, R)	7
ITS	ITS1	ITS4	White et al., 1990	8

Results and Discussion

Phylogenetic Analysis

Tribe Wirthiotremateae was formally established by Lumbsch et al. (2014a) to comprise the *Wirthiotrema, Topeliopsis*, and *Carbacanthographis* clades as defined by Rivas Plata et al. (2013; Fig. 1). While previous analyses mostly showed moderate support for this classification, our analysis using an extended set of six markers suggests that Wirthiotremateae sensu Lumbsch et al. (2014a) can be divided into three well-supported clades (Fig. 2), corresponding largely to those already distinguished by Rivas Plata et al. (2013). These clades are well-distinguished from each other both in morphological and ecological traits: the *Carbacanthographis* clade has lirellate ascomata and is strictly (sub-)tropical, found in warm, humid climates, whereas the *Topeliopsis* and *Wirthiotrema* clades have rounded ascomata; in addition, the *Topeliopsis* clade is tropical-montane to extratropical and often muscicolous, whereas the *Wirthiotrema* clade is, again, (sub-)tropical in warm, humid climates and predominantly corticolous. We therefore propose to limit tribe Wirthiotremateae to the *Wirthiotrema* clade; two new tribes for the other two clades will be established in a forthcoming paper.

The thus newly circumscribed Wirthiotremateae contains two strongly supported clades (Fig. 3): one containing the genus *Wirthiotrema* (*Thelotrema glaucopallens* group) and the other containing the genera *Austrotrema* (newly described for the *Thelotrema bicinctulum* group), *Asteristion* (reinstated for the *Chapsa platycarpa* group), and *Nadvornikia*, with *Austrotrema* being sister to *Asteristion* plus *Nadvornikia*. Except for *Nadvornikia*, these genera each display a rather uniform morphology: *Wirthiotrema* resembles *Myriotrema* in general appearance but differs in having a strongly glossy, often internally splitting cortex, in containing stictic acid, and in producing non-amyloid ascospores; *Austrotrema*, featuring a double apothecial margin, is similar to species of *Thelotrema* with small, immersed ascomata and is difficult to separate morphologically from the latter except for the less distinct paraphyses; and *Asteristion* resembles species of *Chapsa* and related genera, particularly *Astrochapsa*, but differs in the usually well-developed double margin resembling that found in *Thelotrema*. *Nadvornikia* is heterogeneous at this point, as it is accepted here to include mazaediate and non-mazaediate species; the non-mazaediate species *N. peninsulae* and *N. expallescens* agree with the mazaediate *N. hawaiiensis* in certain features, discussed below, but differ clearly in the non-mazaediate ascomata, especially *N. expallescens*, which is more reminiscent of *Austrotrema*. The alternative solution to including these species in *Nadvornikia* would have been to establish two further, monospecific genera, but we opt for the more conservative solution.

Notably, the thus redefined tribe Wirthiotremateae is characterized by a predominance of the stictic acid chemosyndrome (see Table 3), underlying the importance of secondary chemistry at the clade level (Kraichak et al., 2014; Lumbsch et al., 2014b). The stictic acid chemosyndrome, together with the occurrence of periphysoids in several lineages and the variation in ascospore amyloidity and pigmentation, are characters largely shared with tribe Thelotremateae, and a recent study suggests these traits represent symplesiomorphies (Lumbsch et al., 2014b), thus explaining why they are shared by two distantly related clades.

Taxonomic Treatment

Graphidaceae Dumort.

MycoBank #80816

Graphidaceae Dumort. [as 'Graphineae'], Comment. Bot. (Tournay): 69. 1822. Type: *Graphis* Adans.

= Thelotremataceae Stizenb. [as 'Thelotremeae'], Ber. Tät. St Gall naturw. Ges.: 167. 1862. Type: *Thelotrema* Ach.

= Fissurinaceae B. P. Hodk., Opuscula Philolichenum 11: 7. 2012. Type: *Fissurina* Fée.

TABLE 2. GenBank accession numbers for sequences of Wirthiotremateae and allied taxa used in this study. Newly generated sequences are in boldface. All specimens are vouchered at F.

Species	Voucher	mtSSU	nuLSU	RPB1	RPB2	EF1-α	ITS
Acanthothecis peplophora	Common 9126A	JX420954	—	KF688524	—	—	KF688483
Ac. peplophora	Common 9127	JX420955	**KX901737**	—	—	**KX901685**	**KX901711**
Ac. peplophora	Lücking 26501a	HQ639593	HQ639623	—	—	**KX901686**	—
Ac. peplophora	Lücking 26501b	**KX901729**	JX421426	**KX901743**	—	**KX901687**	**KX901721**
Ac. peplophora	Lücking 26503a	JX420953	JX421424	—	—	—	**KX901722**
Ac. peplophora	Lücking 26503b	—	JX421425	—	—	—	—
Ac. poitaeoides	Common 9102	JX420956	**KX901736**	—	—	**KX901688**	**KX901710**
Asteristion alboolivaceum	Lumbsch 19129s	**KX901730**	**KX901738**	**KX901744**	—	**KX901689**	**KX901712**
As. leucophthalmum	Lumbsch 19164q	JX421374	JX421658	**KX901745**	JX420830	—	**KX901713**
As. platycarpum	Lücking 26573	JX421007	JX421460	—	—	—	—
Austrotrema bicinctulum	Mangold 32c	JX421351	—	—	—	—	—
Au. bicinctulum	Mangold 34f	EU075598	EU075642	—	JF828955	—	—
Au. bicinctulum	Mangold 34fb	**KX901731**	**KX901742**	**KX901746**	JX420839	**KX901690**	**KX901724**
Au. terebrans	Lumbsch 20206b	JX421352	JX421647	—	—	—	—
Carbocanthographis chionophora	Rivas Plata 0809A	JF828959	JF828974	—	—	**KX901691**	—
C. stictica	Caceres 6034	JX420967	—	—	JX420882	—	—
C. stictica	Caceres 6040	—	—	—	JF828939	—	—
C. stictica	Rivas Plata 802A	—	JX421435	—	JX420875	**KX901692**	**KX901727**
Heiomasia sipmanii	Nelsen s.n.	GU395552	JX046463	**KX901747**	—	**KX901693**	**KX901728**
Melanotrapelia rugosa	Lumbsch 19383a	HQ639615	—	—	—	—	—
Nadvornikia expallescens	Lücking 15069	—	AY605072	—	—	—	—
N. hawaiiensis	Lumbsch 19176q	—	AY605080	KC020300	—	—	—
N. hawaiiensis	Mangold 36w	EU075581	JX421533	—	—	—	—
N. peninsulae	Lücking 26542	HQ639619	—	—	JF828950	—	—
Schizotrema aff. schizolomum	Mangold 25o	JX421324	**KX901740**	**KX901748**	JX420841	**KX901694**	**KX901720**
S. aff. *zebrinum*	Lumbsch 19983f	JX421326	JX421631	KF875474	—	—	—
S. aff. *zebrinum*	Lumbsch 19983g	JX421325	JX421630	**KX901749**	—	—	—
S. guadeloupense	Mangold 11cI	—	JX421632	**KX901750**	—	—	—
S. schizolomum	Mangold 24c	FJ708500	FJ708492	—	—	—	—
S. schizolomum	Messuti 4743	JX421328	—	—	—	—	—
Schizotrema sp.	Mangold 1g	JX421327	—	**KX901751**	—	—	—
S. subzebrinum	Mangold 19e	—	JX421633	—	—	—	—
S. zebrinum	Mangold 19zo	EU075608	EU075652	—	—	—	—
Topeliopsis acutispora	Lumbsch 19175d	KF875557	JX421675	KF875488	KF875515	**KX901695**	—
T. acutispora	Mangold 13f	—	EU126653	—	—	—	—
T. decorticans	Lumbsch 19984b	KF875558	JX421676	—	KF875516	**KX901697**	**KX901716**
T. decorticans	Lumbsch 19998c	JX421411	—	—	—	—	—
T. decorticans	Lumbsch 19998d	JX421410	—	—	—	—	—
T. decorticans	Lumbsch 20009d	JX421412	—	—	—	—	—
T. decorticans	Mangold 5il	EU075609	EU075654	**KX901752**	KC020285	**KX901696**	—
T. muscigena	Lumbsch 20002e	JX421413	—	—		—	**KX901718**
T. muscigena	Lumbsch 20004d	JX421414	—	**KX901753**	—	**KX901700**	**KX901719**
T. muscigena	Mangold 5d1	EU075611	EU126655	KF875489	JF828957	**KX901698**	—
T. muscigena	Mangold 5d2	—	EU075656	—	—	**KX901699**	—
T. muscigena	Mangold 5ill	**KX901732**	EU126654	—	—	—	**KX901726**
Topeliopsis sp.	Lumbsch 20002d	JX421415	—	**KX901754**	—	**KX901701**	**KX901717**
T. subdenticulata	Knight 59967	KF875559	EU126656	KF875490	KF875517	—	—
T. subdenticulata	Lumbsch 19998h	JX421416	—	—	—	—	—
Wirthiotrema desquamans	Lumbsch 19166o	**KX901734**	AY605085	—	—	—	—
W. desquamans	Lumbsch 19167v	EU075580	EU075628	**KX901755**	—	**KX901702**	**KX901715**
W. desquamans	Lumbsch 20205c	—	JX421680	—	—	—	—
W. desquamans	Lumbsch 20520a1	JX421419	—	—	—	—	—
W. desquamans	Lumbsch 20521i	JX421420	JX421677	—	—	—	—
W. desquamans	Mangold 32zb	JX421418	**KX901741**	—	—	**KX901703**	**KX901723**
W. desquamans	Rivas Plata 2014	**KX901733**	JX421679	**KX901756**	—	**KX901704**	**KX901709**
W. duplomarginatum	Lumbsch 19167c	JF828972	**KX901739**	—	—	**KX901705**	**KX901714**
W. duplomarginatum	Mangold 34s	JX421417	KF875536	KF875491	KF875518	**KX901706**	**KX901725**
W. glaucopallens	Lücking 15620	—	AY605069	—	—	—	—
W. santessonii	Frisch 99Ka1628	DQ384907	—	—	—	—	—
W. santessonii	Frisch 99Ka445	DQ384908	—	—	—	—	—
W. santessonii	Frisch 99Ka471	DQ384906	—	—	—	—	—
W. trypaneoides	Lücking 32003	JX421422	JX421681	—	JX420916	—	—

Wirthiotremateae Lumbsch, Kraichak & Lücking

MycoBank #807540

Wirthiotremateae Lumbsch, Kraichak & Lücking in Lumbsch et al., Phytotaxa 189: 47. 2014. Type: *Wirthiotrema* Rivas Plata, Kalb, Frisch & Lumbsch.

DESCRIPTION—Thallus corticolous, epiperidermal, smooth to uneven; prothallus absent. Cortex generally present (absent in two species); photobiont layer and medulla usually with calcium oxalate crystals. Photobiont *Trentepohlia*, cells rounded to irregular or elongate in outline, in irregular groups, brown- to olive-green, 3–10 × 4–12 µm. Ascomata round,

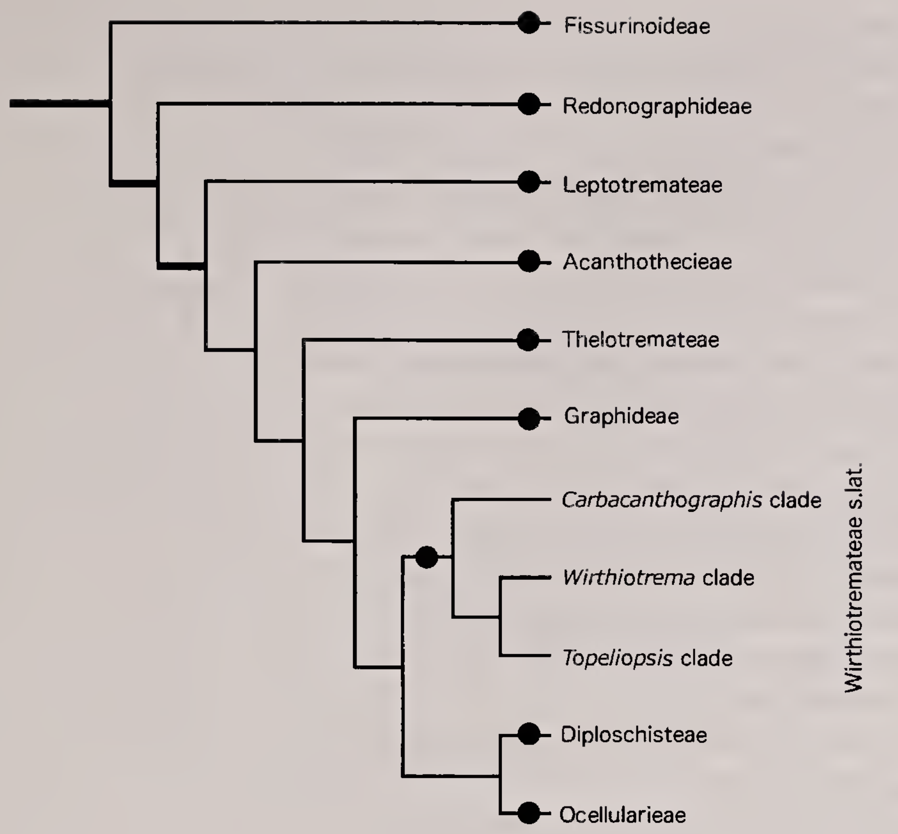

FIG. 1. Phylogeny of Graphidaceae based on tree from Kraichak et al. (2015a), with tribe classification according to Lumbsch et al. (2014a). Note that while Lumbsch et al. (2014) found support for all tribes under their classification scheme (black circles), only the early-diverging branches have a supported backbone (thickened branches); the backbone of the core Graphidaceae is poorly resolved. Lumbsch et al. (2014) did not find support for clades within their tribe Wirthiotremateae, except for the *Wirthiotrema* clade.

occasionally becoming angular, generally immersed to erumpent but prominent to sessile in three species. Ascospores various. Secondary chemistry: stictic acid (major), occasionally accompanied by constictic acid (major), with a variety of stictic acid chemosyndrome compounds (β-orcinol depsidones) as minor or trace substances.

DISCUSSION—This tribe was formally established by Lumbsch et al. (2014a) to include the *Carbacanthographis*, *Topeliopsis*, and *Wirthiotrema* clades of Rivas Plata et al. (2013). Based on our extended phylogenetic analysis, it is here limited to the *Wirthiotrema* clade sensu Rivas Plata et al. (2013). Tribe Wirthiotremateae is similar in morphology and chemistry to tribe Thelotremateae and apparently both tribes feature largely plesiomorphic characters, being part of a paraphyletic assemblage of lineages basal to the large tribes Graphideae and Ocellularieae (Rivas Plata et al., 2013; Lumbsch et al., 2014a).

KEY TO GENERA—The following complementary key refers to the genus key provided by Rivas Plata et al. (2010b), placing the two newly recognized genera and the non-mazaediate species of *Nadvornikia* at the corresponding key couplets. The mazaediate species of *Nadvornikia* are not treated in this key.

Couplet 8(7) in Rivas Plata et al. (2010b: 150), first alternative (*Thelotrema*):

1A. Thallus with more or less dense cortex; ascospores up to 60 μm long; stictic acid 2
   2A. Apothecia >0.3-mm diam., erumpent to prominent, with thick, often fissured thalline margin; periphysoids distinct .... ***Asteristion* Leight.**
   2B. Apothecia to 0.3-mm diam., immersed-erumpent, with thin, entire thalline margin; periphysoids indistinct .... ***Austrotrema* I. Medeiros, Lücking & Lumbsch**
1B. Thallus with different combination of characters, not at the same time with dense cortex and stictic acid .... ***Thelotrema* Ach.**

Couplet 10(9) in Rivas Plata et al. (2010b: 150), second alternative (*Chapsa*):

1A. Apothecia with free excipulum and distinct double margin; thallus with dense cortex; stictic acid .... ***Asteristion* Leight.**
1B. Apothecia with fused excipulum; cortex and chemistry variable .... ***Chapsa* s.l.** (1B also includes the recently segregated genera *Astrochapsa* Parnmen, Lücking & Lumbsch and *Pseudochapsa* Parnmen, Lücking & Lumbsch)

Couplet 18(17) in Rivas Plata et al. (2010b: 151), second alternative (*Leucodecton*):

1A. Apothecia distinctly lepadinoid, erumpent to prominent, >0.3-mm diam.; ascospores hyaline .... ***Nadvornikia* Tibell, p.p.**
1B. Apothecia porinoid, myriotremoid or small-lepadinoid, immersed-erumpent, generally up to 0.3-mm diam.; ascospores mostly brown, if remaining hyaline then apothecia not lepadinoid .... ***Leucodecton* A. Massal.**

Asteristion Leight.

MycoBank #416

Asteristion Leight., Trans. Linn. Soc. London 27: 163. 1870; *Thelotrema* sect. *Asteristion* (Leight.) Tat. Matsumoto, J. Hattori Bot. Lab. 88: 16. 2000; *Asteristium* Clements, The Genera of Fungi: 76. 1909 [nom. illeg.]. Type species: *Asteristion erumpens* Leight. [= *Asteristion platycarpum* (Tuck.) I. Medeiros, Lücking & Lumbsch].

DESCRIPTION—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven; prothallus absent. Thallus with a loose to prosoplectenchymatous cortex, with photobiont layer interspersed with calcium oxalate crystals, and thin epi- to endoperidermal medulla. Photobiont *Trentepohlia*. Ascomata rounded to angular, immersed to erumpent; disc covered to exposed, flesh-colored to brown, white-pruinose; proper margin distinct, fissured to recurved, separated from the thalline margin by a narrow split (double margin), forming a prominent rim around the disc; thalline margin white to pale brown, entire to recurved. Excipulum entire, hyaline to pale yellow, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present; asci fusiform. Ascospores fusiform to ellipsoid, transversely septate to muriform, (sub-)distoseptate with lens-shaped lumina, hyaline to brown, I− to I+. Conidiomata not observed. Secondary chemistry stictic acid (major) and associated satellite substances (minor to trace).

ETYMOLOGY—The genus name refers to the star-like appearance of the recurved thalline margin common in this genus and particularly visible in the type species.

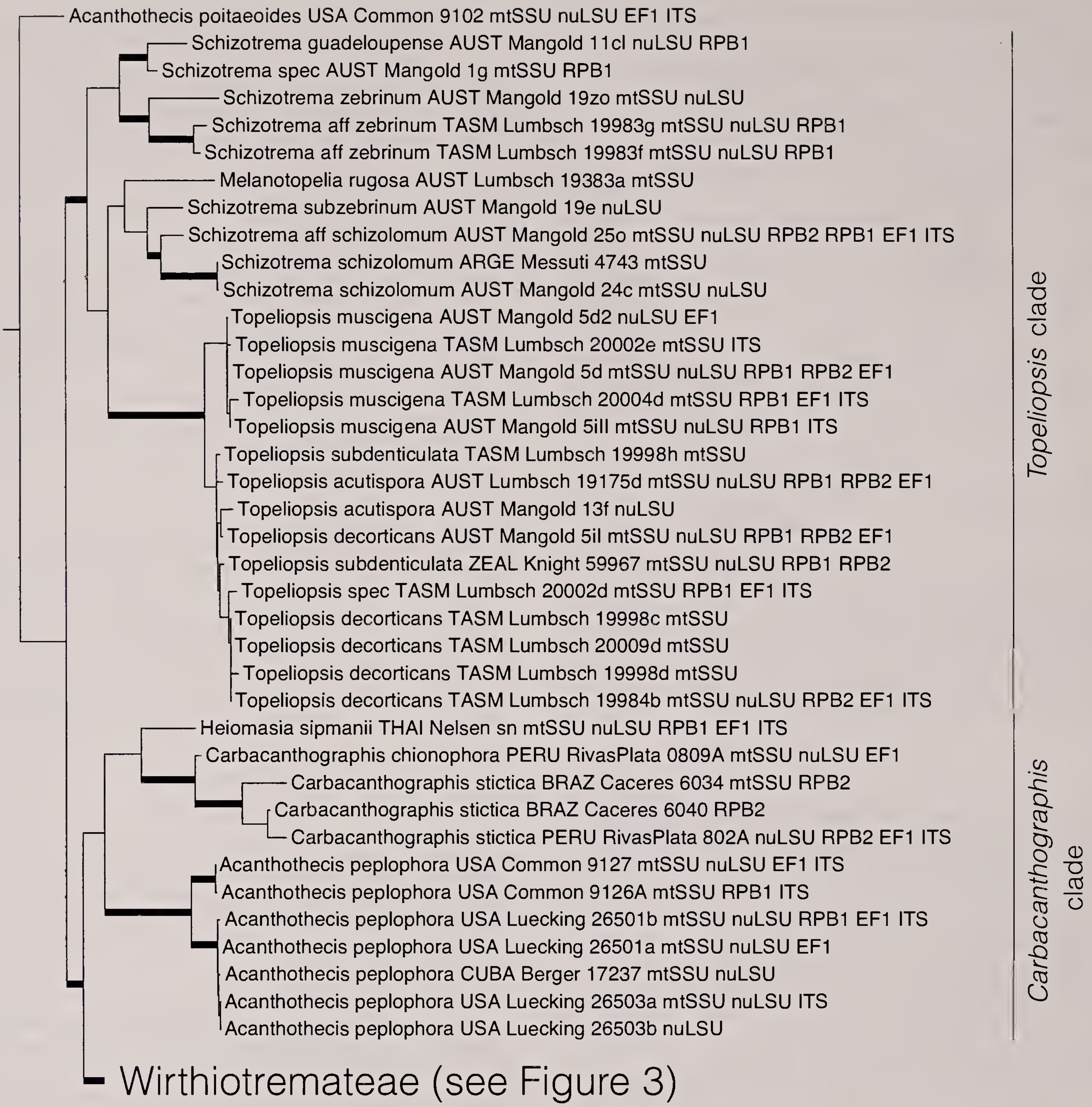
Acanthothecis poitaeoides USA Common 9102 mtSSU nuLSU EF1 ITS
Schizotrema guadeloupense AUST Mangold 11cl nuLSU RPB1
Schizotrema spec AUST Mangold 1g mtSSU RPB1
Schizotrema zebrinum AUST Mangold 19zo mtSSU nuLSU
Schizotrema aff zebrinum TASM Lumbsch 19983g mtSSU nuLSU RPB1
Schizotrema aff zebrinum TASM Lumbsch 19983f mtSSU nuLSU RPB1
Melanotopelia rugosa AUST Lumbsch 19383a mtSSU
Schizotrema subzebrinum AUST Mangold 19e nuLSU
Schizotrema aff schizolomum AUST Mangold 25o mtSSU nuLSU RPB2 RPB1 EF1 ITS
Schizotrema schizolomum ARGE Messuti 4743 mtSSU
Schizotrema schizolomum AUST Mangold 24c mtSSU nuLSU
Topeliopsis muscigena AUST Mangold 5d2 nuLSU EF1
Topeliopsis muscigena TASM Lumbsch 20002e mtSSU ITS
Topeliopsis muscigena AUST Mangold 5d mtSSU nuLSU RPB1 RPB2 EF1
Topeliopsis muscigena TASM Lumbsch 20004d mtSSU RPB1 EF1 ITS
Topeliopsis muscigena AUST Mangold 5ill mtSSU nuLSU RPB1 ITS
Topeliopsis subdenticulata TASM Lumbsch 19998h mtSSU
Topeliopsis acutispora AUST Lumbsch 19175d mtSSU nuLSU RPB1 RPB2 EF1
Topeliopsis acutispora AUST Mangold 13f nuLSU
Topeliopsis decorticans AUST Mangold 5il mtSSU nuLSU RPB1 RPB2 EF1
Topeliopsis subdenticulata ZEAL Knight 59967 mtSSU nuLSU RPB1 RPB2
Topeliopsis spec TASM Lumbsch 20002d mtSSU RPB1 EF1 ITS
Topeliopsis decorticans TASM Lumbsch 19998c mtSSU
Topeliopsis decorticans TASM Lumbsch 20009d mtSSU
Topeliopsis decorticans TASM Lumbsch 19998d mtSSU
Topeliopsis decorticans TASM Lumbsch 19984b mtSSU nuLSU RPB2 EF1 ITS
Heiomasia sipmanii THAI Nelsen sn mtSSU nuLSU RPB1 EF1 ITS
Carbacanthographis chionophora PERU RivasPlata 0809A mtSSU nuLSU EF1
Carbacanthographis stictica BRAZ Caceres 6034 mtSSU RPB2
Carbacanthographis stictica BRAZ Caceres 6040 RPB2
Carbacanthographis stictica PERU RivasPlata 802A nuLSU RPB2 EF1 ITS
Acanthothecis peplophora USA Common 9127 mtSSU nuLSU EF1 ITS
Acanthothecis peplophora USA Common 9126A mtSSU RPB1 ITS
Acanthothecis peplophora USA Luecking 26501b mtSSU nuLSU RPB1 EF1 ITS
Acanthothecis peplophora USA Luecking 26501a mtSSU nuLSU EF1
Acanthothecis peplophora CUBA Berger 17237 mtSSU nuLSU
Acanthothecis peplophora USA Luecking 26503a mtSSU nuLSU ITS
Acanthothecis peplophora USA Luecking 26503b nuLSU
Topeliopsis clade
Carbacanthographis clade
Wirthiotremateae (see Figure 3)

FIG. 2. Phylogenetic tree (maximum likelihood) showing Wirthiotremateae with respect to neighboring clades. Thickened branches indicate ≥90% bootstrap support. The "*Carbacanthographis* clade" has 88% bootstrap support. Sequenced loci are listed for each specimen.

DISCUSSION—*Asteristion* was long considered a synonym of either *Phaeotrema* (based on ascospore type) or *Thelotrema* (based on excipulum type; Hale, 1980); it was recognized as a section of *Thelotrema* Ach. by Matsumoto (2000). Molecular evidence (Rivas Plata et al., 2013) demonstrated that the type species, *A. erumpens* Leight. [= *A. platycarpum* (Tuck.) I. Medeiros, Lücking & Lumbsch] does not belong in *Thelotrema* or any other currently recognized genus, and since based on our extended phylogenetic analysis several other species are closely related to the type, the genus *Asteristion* is resurrected here for this group. *Asteristion* species are distinguished within Wirthiotremateae by their large, often chroodiscoid ascomata and by the presence of distinct periphysoids (lateral paraphyses). Species of *Asteristion* (particularly the type species) may resemble *Chapsa* and allies, such as *Astrochapsa*, but can be distinguished from those genera by the presence of a distinctly free excipulum forming a double margin (versus a fused excipulum in *Chapsa*). As circumscribed here, the genus contains seven species.

KEY TO SPECIES

1A. Ascospores weakly to strongly amyloid (I+ faint to intense blue-violet), transversely septate to submuriform, hyaline or brown 2
  2A. Ascospores hyaline 3
    3A. Ascospores 3-septate, up to 6 μm broad .... ***A. albo-olivaceum***
    3B. Ascospores submuriform, up to 8 μm broad.. 4
      4A. Ascospores 10–15 μm long, with 3 transverse septa .... ***A. alboannuliforme***

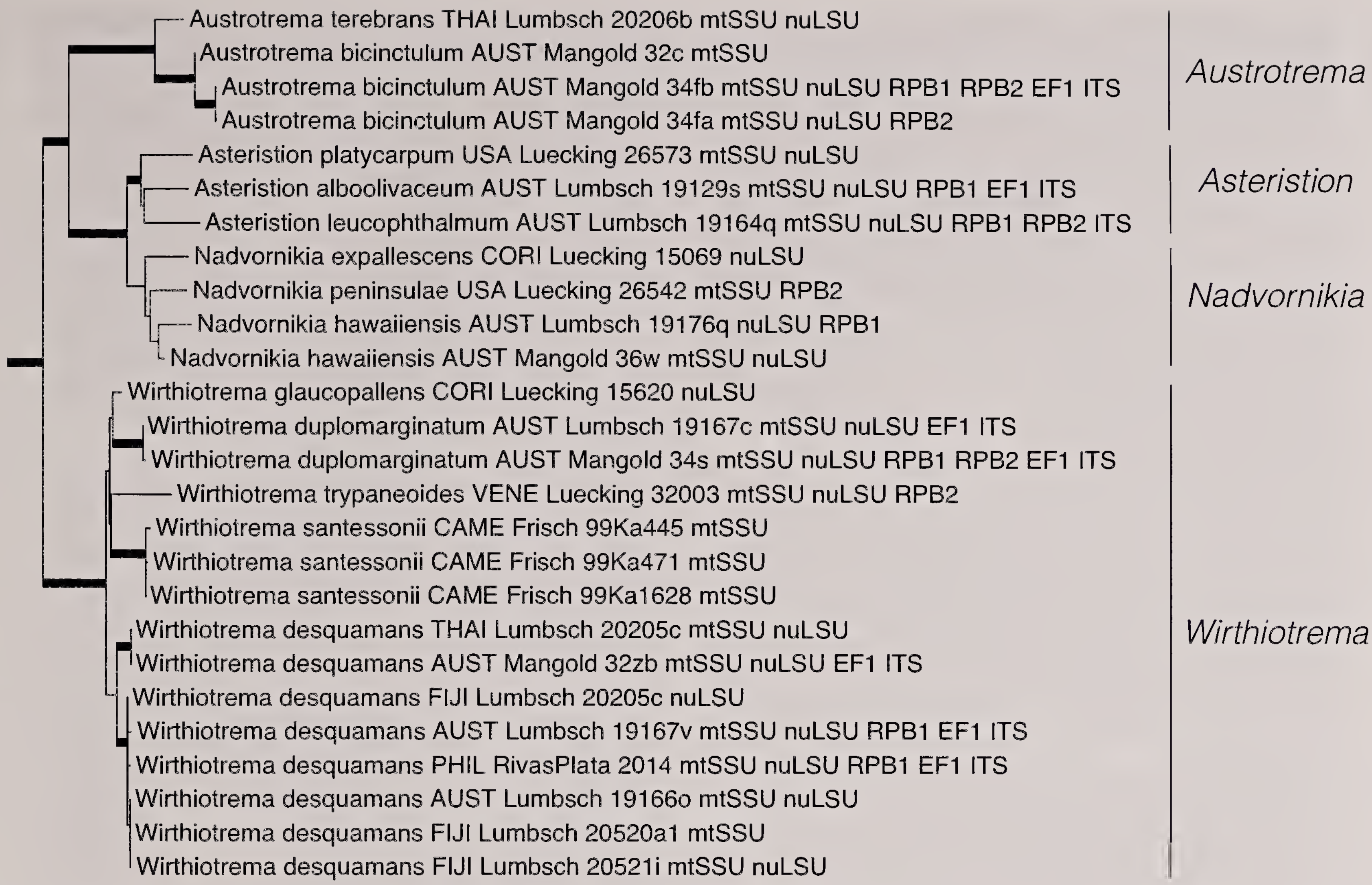
Austrotrema terebrans THAI Lumbsch 20206b mtSSU nuLSU
Austrotrema bicinctulum AUST Mangold 32c mtSSU
Austrotrema bicinctulum AUST Mangold 34fb mtSSU nuLSU RPB1 RPB2 EF1 ITS
Austrotrema bicinctulum AUST Mangold 34fa mtSSU nuLSU RPB2
Asteristion platycarpum USA Luecking 26573 mtSSU nuLSU
Asteristion alboolivaceum AUST Lumbsch 19129s mtSSU nuLSU RPB1 EF1 ITS
Asteristion leucophthalmum AUST Lumbsch 19164q mtSSU nuLSU RPB1 RPB2 ITS
Nadvornikia expallescens CORI Luecking 15069 nuLSU
Nadvornikia peninsulae USA Luecking 26542 mtSSU RPB2
Nadvornikia hawaiiensis AUST Lumbsch 19176q nuLSU RPB1
Nadvornikia hawaiiensis AUST Mangold 36w mtSSU nuLSU
Wirthiotrema glaucopallens CORI Luecking 15620 nuLSU
Wirthiotrema duplomarginatum AUST Lumbsch 19167c mtSSU nuLSU EF1 ITS
Wirthiotrema duplomarginatum AUST Mangold 34s mtSSU nuLSU RPB1 RPB2 EF1 ITS
Wirthiotrema trypaneoides VENE Luecking 32003 mtSSU nuLSU RPB2
Wirthiotrema santessonii CAME Frisch 99Ka445 mtSSU
Wirthiotrema santessonii CAME Frisch 99Ka471 mtSSU
Wirthiotrema santessonii CAME Frisch 99Ka1628 mtSSU
Wirthiotrema desquamans THAI Lumbsch 20205c mtSSU nuLSU
Wirthiotrema desquamans AUST Mangold 32zb mtSSU nuLSU EF1 ITS
Wirthiotrema desquamans FIJI Lumbsch 20205c nuLSU
Wirthiotrema desquamans AUST Lumbsch 19167v mtSSU nuLSU RPB1 EF1 ITS
Wirthiotrema desquamans PHIL RivasPlata 2014 mtSSU nuLSU RPB1 EF1 ITS
Wirthiotrema desquamans AUST Lumbsch 19166o mtSSU nuLSU
Wirthiotrema desquamans FIJI Lumbsch 20520a1 mtSSU
Wirthiotrema desquamans FIJI Lumbsch 20521i mtSSU nuLSU
Austrotrema
Asteristion
Nadvornikia
Wirthiotrema

FIG. 3. Detailed phylogeny (maximum likelihood) of the Wirthiotremateae. Thickened branches indicate ≥90% bootstrap support. Sequenced loci are listed for each specimen.

4B. Ascospores 15–23 µm long, with 3–5 transverse septa .... ***A. australianum***

2B. Ascospores brown, transversely septate 5

5A. Apothecia large; thalline margin recurved, UV–; disc exposed; ascospores predominantly 3-septate .... ***A. platycarpum***

5B. Apothecia small; thalline margin entire fissured, often UV+ faintly yellow; disc partly covered; ascospores predominantly 5-septate .... ***A. platycarpoides***

1B. Ascospores non-amyloid (I–), (sub-)muriform, hyaline 6

6A. Ascospores 15–30 µm long; cortex prosoplectenchymatous; ascomata often aggregate .... ***A. cupulare***

6B. Ascospores 30–60 µm long; cortex loose and irregular; ascomata usually solitary.. ***A. leucophthalmum***

TABLE 3. Elements of the stictic acid chemosyndrome reported from species of tribe Wirthiotremateae. Thin-layer chromatography (TLC) R_f values provided for Solvent C (170 parts toluene:30 parts glacial acetic acid), the standard general-purpose solvent for lichen TLC, and Solvent G (139 parts toluene:83 parts ethyl acetate:8 parts formic acid), a useful solvent for separating out molecules with low R_f values in Solvent C. TLC data from Orange et al. (2010) and Elix (2014). "Color" refers to the color of the substance after the TLC plate has been treated with H_2SO_4 and baked at 110°C.

Substance	R_f C	R_f G	Color
Cryptoconstictic acid	1	6	orange
Consalazinic acid	1	6	orange
Constictic acid	2	9	orange-brown
Hypoconstictic acid	4	28	dark red
Cryptostictic acid	10	27	orange
Acetylconstictic acid	11	23	orange-red
Stictic acid	18	34	orange
Acetylhypoconstictic acid	20	46	pale red
Hypostictic acid	32	61	pale red

Asteristion alboannuliforme **(Nagarkar, Sethy & Patwardhan) I. Medeiros, Lücking & Lumbsch, comb. nov.**

MycoBank #818200

Basionym: *Thelotrema alboannuliforme* Nagarkar, Sethy & Patwardhan, Kavaka 13: 57. 1985. Type: India, Tamil Nadu, Tirunelvelli District, Singhalamatheri, Patwardhan & Sethy 84.9 (AMH, holotype, not seen; US!, isotype).

DESCRIPTION—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, grayish olive; prothallus absent. Thallus in section up to 250 µm thick, cortex dense, prosoplectenchymatous, up to 50 µm thick, with irregular photobiont layer containing abundant calcium oxalate crystals, and indistinct medulla. Photobiont *Trentepohlia*. Ascomata erumpent, round to angular, 0.6- to 0.8-mm diam.; disc more or less covered by 0.2- to 0.3-mm-wide pore, pale gray-brown, white-pruinose; proper margin distinct, entire to slightly fissured, separated from the thalline margin by a narrow split (double margin), forming a white rim around the disc; thalline margin entire to slightly fissured, eroding. Excipulum hyaline, with gray crystals on apical surface, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium up to 120 µm high, hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present, smooth, up to 20 µm; asci fusiform. Ascospores 8 per ascus, ellipsoid, submuriform with 3 transverse and 0–1 longitudinal septa per segment, 10–15 × 5–8 µm, 1.8–2.3 times long as wide, hyaline, distoseptate, I+ strongly amyloid. Conidiomata not observed. Secondary chemistry stictic and constictic acids (major). Microscopic section with K+ yellow efflux (sometimes indistinct).

ILLUSTRATION—Nagarkar et al. (1985). Page 61, figure 1: Photograph of fertile thallus (holotype).

ETYMOLOGY—The epithet references the apothecial margin forming a white ring around the pore.

DISTRIBUTION AND ECOLOGY—*Asteristion alboannuliforme* is known from primary lower montane rain forest in the state of Tamil Nadu in India (Nagarkar et al., 1985).

DISCUSSION—*Asteristion alboannuliforme* is here included in *Asteristion* due to the striking similarities with *A. albo-olivaceum* and *A. australianum*, the latter two placed in this genus based on sequence data. All three species have similar apothecial morphology and distinctly amyloid ascospores and share with the other species of the genus the stictic acid chemistry. *Asteristion alboannuliforme* differs from *A. albo-olivaceum* in the shorter and broader, submuriform ascospores and from *A. australianum* in the shorter ascospores and mostly entire apothecial margins.

SPECIMENS EXAMINED—**INDIA**. The isotype.

Asteristion albo-olivaceum **(Vain.) I. Medeiros, Lücking & Lumbsch, comb. nov.**

Figure 4A–D

MycoBank #818201

Basionym: *Thelotrema albo-olivaceum* Vain., Mycologia 21: 38. 1929 [as alboolivaceum]; *Ocellularia albo-olivacea* (Vain.) Zahlbr., Cat. Lich. Univ. 8: 244. 1931 [as alboolivacea]. Type: Puerto Rico, near Vega Baja, Fink 2153 (TUR-VAIN 34714!, holotype; FH!, MICH!, NY!, isotypes).

DESCRIPTION—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, occasionally slightly verruculose, light grayish to yellowish-olive; prothallus absent. Thallus in section up to 100 µm thick, cortex dense, prosoplectenchymatous, up to 35 µm thick, with irregular photobiont layer containing abundant calcium oxalate crystals, and indistinct medulla. Photobiont *Trentepohlia*. Ascomata erumpent, round to angular, 0.3- to 0.7-mm diam.; disc more or less covered by 0.2- to 0.4-mm-wide pore, pale gray-brown, white-pruinose; proper margin distinct, fissured, separated from the thalline margin by a narrow split (double margin), forming a white rim around the disc; thalline margin entire to rarely slightly fissured. Excipulum hyaline, with gray crystals on apical surface, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium up to 100 µm high, hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present, smooth, up to 25 µm; asci fusiform. Ascospores 8 per ascus, fusiform to claviform, 3-septate, 15–20 × 5–6 µm, 3–4 times long as wide, hyaline, distoseptate, I+ strongly amyloid. Conidiomata not observed. Secondary chemistry stictic and constictic acids (major) and acetylconstictic and cryptoconstictic acids (minor). Microscopic section with K+ yellow efflux (sometimes indistinct).

ILLUSTRATION—Mangold et al. (2009). Page 359, figure 115, A: Photograph of fertile thallus (holotype).

ETYMOLOGY—The epithet references the whitish apothecia contrasting with the olive thallus.

DISTRIBUTION AND ECOLOGY—*Asteristion albo-olivaceum* is known with certainty only from Puerto Rico. The recent report from Australia pertains to a previously undescribed species, *A. australianum* (see below). We have not been able to verify the reports from India and Sri Lanka (Patwardhan & Kulkarni, 1977; Singh & Sinha, 2010), which may actually represent the new *A. australianum*. *Asteristion albo-olivaceum* was reported by Vainio (1929: 38) as "on bark in woods" and likely is a rare understory taxon restricted to well-preserved rain forest. Material identified as *Thelotrema alboolivaceum* [sic!] was used by Lakatos et al. (2006) to study the ecomorphological adaptations of rain forest lichens to low light levels. However, judging from the habit photograph of the lichen in question (Lakatos et al. 2006: 685), it is not that taxon but either *Astrochapsa zahlbruckneri* (Redinger) Parnmen, Lücking & Lumbsch, which also contains stictic acid but produces muriform, non-amyloid ascospores, or (less likely) a species of *Rhabdodiscus*, such as *R. emersus* (Kremp.) Rivas Plata, Lücking & Lumbsch, which can be distinguished by the carbonized excipulum and columella and the psoromic acid chemistry.

DISCUSSION—*Asteristion albo-olivaceum* is characterized by *Thelotrema*-like apothecia with a more or less entire thalline rim and by the consistently 3-septate, strongly amyloid ascospores. The concept of the species was emended by Mangold et al. (2009) to include material from Australia with broader, submuriform ascospores. However, considering the difference in ascospore septation and width and the fact that the Australian material has apothecia with a fissured to lobulate thalline rim, plus the quite distinct distribution, we see no alternative to describing the Australian population as a separate species, *A. australianum* (see below). Morphologically most similar to *A. albo-olivaceum* is *A. platycarpoides*, which agrees in apothecia morphology but has brown, predominantly 5-septate ascospores. While both species resemble *Thelotrema*, most species of the latter genus can be separated by the lack of a dense thallus cortex and by their different ascospores. Most similar is *T. triseptatum* Mangold, Flora of Australia 57: 658 (2009), which agrees in the 3-septate, amyloid ascospores and the stictic acid chemistry but differs in the whitish, ecorticate thallus and the narrow apothecial pore.

SPECIMENS EXAMINED—**USA**. Puerto Rico: The holotype and isotypes.

Asteristion australianum **I. Medeiros, Lücking, Mangold & Lumbsch, sp. nov.**

Figure 4E–F

MycoBank #818202

Differing from *Asteristion albo-olivaceum* in the broader, submuriform ascospores. Type: Australia, Queensland, Atherton Tableland, Malanda Falls, Lumbsch & Mangold 19129s (BRI!, holotype; F!, isotype).

DESCRIPTION—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, olive-brown; prothallus absent. Thallus in section up to 100 µm thick, cortex dense,

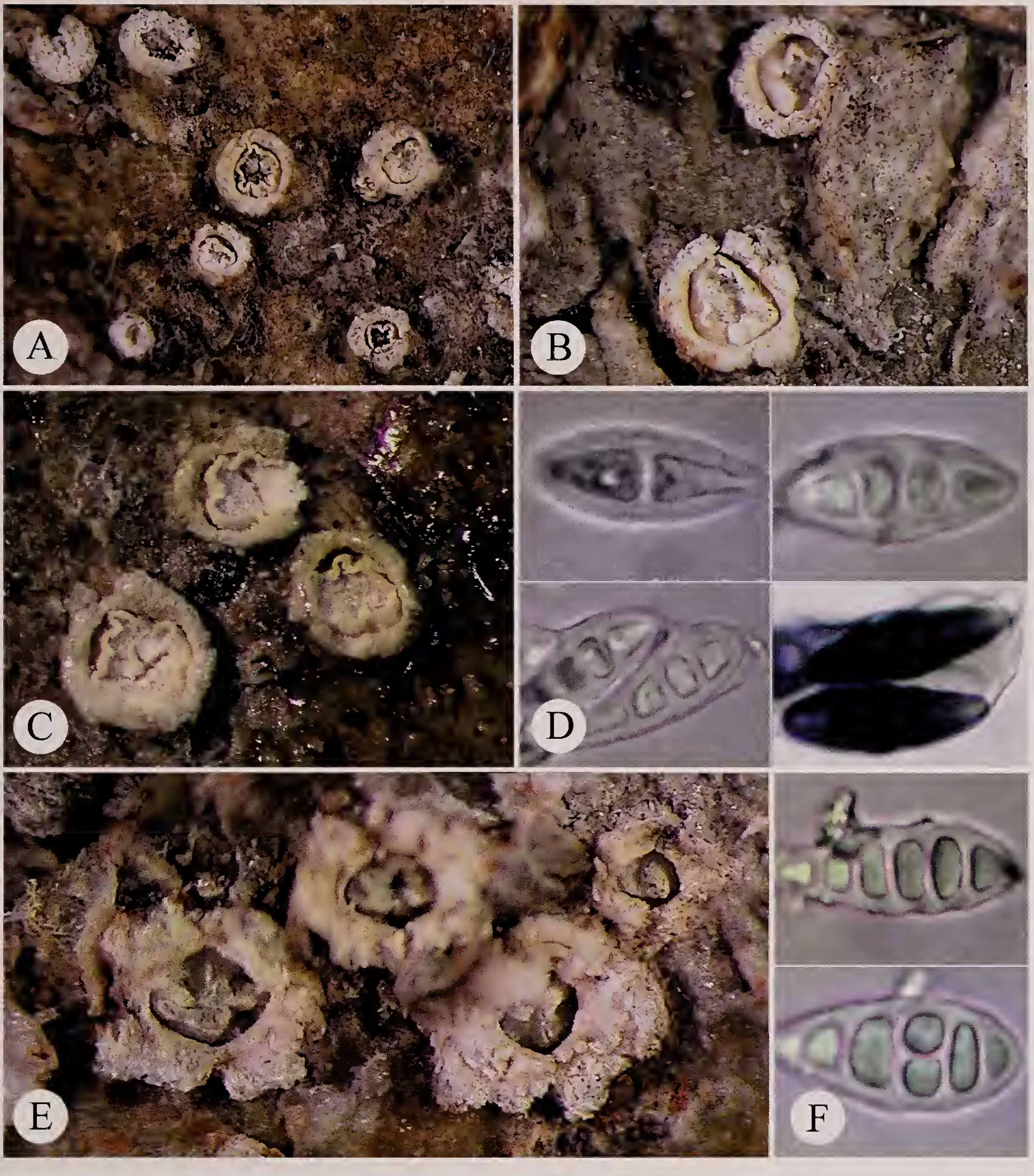

FIG. 4. Morphology and anatomy in Wirthiotremateae. (**A–D**) *Asteristion albo-olivaceum* (A–B, D: holotype; C: isotype in NY); A–C, thallus with apothecia; D, ascospores, in part showing I+ amyloid reaction. (**E–F**) *A. australianum* (holotype); E, thallus with ascomata; F, ascospores.

prosoplectenchymatous, up to 30 µm thick, with irregular photobiont layer containing abundant calcium oxalate crystals, and indistinct medulla. Photobiont *Trentepohlia*. Ascomata erumpent, round to angular, 0.4- to 0.7-mm diam.; disc more or less covered by 0.2- to 0.4-mm-wide pore, pale gray-brown, white-pruinose; proper margin distinct, fissured, separated from the thalline margin by a narrow split (double margin), forming a white rim around the disc; thalline margin fissured to lobulate. Excipulum hyaline, with gray crystals on apical surface, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium up to 100 µm high, hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present, smooth, up to 25 µm; asci fusiform. Ascospores 8 per ascus, fusiform to claviform, submuriform with 3–5 transverse and 0–1 longitudinal septa per segment, 15–23 × 6–8 µm, 2.5–3 times long as wide, hyaline, distoseptate, I+ amyloid. Conidiomata not observed. Secondary chemistry stictic and constictic acids (major) and acetylconstictic and cryptoconstictic acids (minor). Microscopic section with K+ yellow efflux (sometimes indistinct).

ILLUSTRATION—Mangold et al. (2009). Page 359, figure 115, B: Photograph of ascospore of *Thelotrema albo-olivaceum* (holotype).

ETYMOLOGY—The epithet refers to the distribution of the new species.

DISTRIBUTION AND ECOLOGY—*Asteristion australianum* is a tropical rain forest species known thus far only from Australia.

DISCUSSION—*Asteristion australianum* was first identified with the Puerto Rican species *A. albo-olivaceum* (see above) by Mangold et al. (2009). However, the morphological differences in the apothecial margin and the broader, submuriform versus 3-septate ascospores, together with the different distribution, justify its recognition as a separate taxon. Similar cases within Graphidaceae where a broad species concept had been applied to material from different tropical regions without exception turned out to represent several distinct species in molecular phylogenetic studies, whereas truly pantropical taxa were found remarkably uniform in their phenotypic features (Rivas Plata et al., 2013). Unfortunately, we were unable to verify the reports of *Thelotrema albo-olivaceum* from India and Sri Lanka (Patwardhan & Kulkarni, 1977; Singh & Sinha, 2010). Most likely these do not represent that species, but there is a possibility that they are conspecific with *A. australianum*: The ascospore measurements reported by Patwardhan and Kulkarni (1977), 5–6-septate and 4–8 × 11–20 µm, agree more with *A. australianum* than with *A. albo-olivaceum*. However, Patwardhan and Kulkarni (1977) describe the spores of their *Ocellularia albo-olivacea* as being inamyloid, while the spores of both *A. australianum* and *A. albo-olivaceum* are amyloid. It should be noticed that at the time these identifications were made, no good keys were available for thelotremoid Graphidaceae and hence misidentifications even with unrelated taxa, or the possibility that these reports represent an undescribed species, cannot be excluded.

SPECIMENS EXAMINED—**AUSTRALIA**. The holotype and isotype.

Asteristion cupulare (Müll. Arg.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 5A–D

MycoBank #818203

Basionym: *Thelotrema cupulare* Müll. Arg., Hedwigia 32: 131. 1893. Type: Australia, Queensland, near Brisbane, Bailey 375 (G!, holotype; BRI!, isotype).

Thelotrema dissultum Hale, Bull. Br. Mus. Nat. Hist., Bot. 8(3): 254. 1981. Type: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Halwathura-Kanda, Hale 51139 (US!, holotype).

DESCRIPTION—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, yellowish-olive, waxy; prothallus absent. Thallus in section up to 200 µm thick, cortex dense, prosoplectenchymatous, up to 100 µm thick, with irregular photobiont layer containing abundant calcium oxalate crystals, and indistinct medulla. Photobiont *Trentepohlia*. Ascomata erumpent, round to angular, often aggregate or with several discs formed in the same apothecium, 1- to 1.8-mm diam.; disc more or less exposed beneath 0.6- to 1.2-mm-wide pore, flesh-colored, white-pruinose; proper margin distinct, recurved, separated from the thalline margin by a narrow split (double margin), forming a white rim around the disc; thalline margin entire to fissured or becoming lobulate, erect to recurved, white-pruinose. Excipulum hyaline, with gray crystals on apical surface, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium up to 100 µm high, hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present to indistinct, smooth, up to 20 µm; asci fusiform. Ascospores 8 per ascus, ellipsoid, (sub-)muriform, with 5–7 transverse septa and 0–2 longitudinal septa per segment, 15–30 × 5–10 µm, 3 times long as wide, hyaline, distoseptate, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic acid (major) and acetylconstictic and constictic acids (minor). Microscopic section with visible to indistinct K+ yellow efflux.

ILLUSTRATIONS—Hale (1981). Page 252, figure 7, g: Photograph of fertile thallus (holotype of *Thelotrema dissultum*). Mangold et al. (2009). Page 368, figure 122: Photograph of fertile thallus (holotype) and ascospores (Australian collection).

ETYMOLOGY—The epithet refers to the shape of the apothecia, which become deeply concave as they mature.

DISTRIBUTION AND ECOLOGY—*Asteristion cupulare* has a paleotropical distribution, with several collections reported from Australia (Mangold et al., 2009), New Caledonia (examined specimen), and Sri Lanka (as *Thelotrema dissultum*; Hale, 1981). It occurs in well-preserved lowland rain forests.

DISCUSSION—We do not yet have molecular data for this species, but based on phenotypical characters it is closely related to *Asteristion leucophthalmum*. Both have hyaline, muriform, non-amyloid ascospores and flesh-colored, white-pruinose ascomatal discs, features that are not found together in any other species in the genus. *Asteristion cupulare* can be distinguished from *A. leucophthalmum* on the basis of its smaller ascospores (15–30 µm long and submuriform versus 30–60 µm long and muriform). The only other member of Wirthiotremateae that occasionally forms aggregate ascomata is *A. platycarpoides*, which has smaller ascomata and smaller, 5-septate, brown ascospores. Mangold et al. (2009) noted that *A. cupulare* is similar in appearance to *Thelotrema thesaurum* Mangold, Flora of Australia 57: 658 (2009), but the latter has much larger ascospores and a narrow apothecial pore.

SPECIMENS EXAMINED—**AUSTRALIA**. The holotype and isotype. Queensland, various localities in the eastern part of the state: All specimens cited by Mangold et al. (2009). **NEW CALEDONIA**. Papong & Lumbsch 8214 (F, IRD). **SRI LANKA**. The holotype of *Thelotrema dissultum* and other specimens cited under *Thelotrema dissultum* by Hale (1981).

Asteristion leucophthalmum (Nyl.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 5E–G

MycoBank #818204

Basionym: *Thelotrema leucophthalmum* Nyl., Syn. Lich. Novae Caledoniae: 39. 1868. Type: New Caledonia, Loyalty Islands, Lifou, Thiébaut s.n. (H-NYL 22518!, lectotype fide Hale, in herb. 1972).

Leptotrema albocoronatum [as *albo-coronata*] C. Knight in Shirley, Proc. R. Soc. Qd. 6: 192. 1889. Type: Australia, Queensland, Sankey's Scrub [Brisbane], Shirley 509 (WELT!, lectotype fide Mangold et al., 2009: 658; BRI!, isolectotype).

Thelotrema leucophthalmum var. *annulare* [as *annularis*] Räsänen, Arch. Soc. Zool. Bot. Fenn. "Vanamo" 3: 184. 1949. Type: Vanuatu (New Hebrides), Aneityum, Wilson s.n. (H!, holotype).

DESCRIPTION—Thallus corticolous, epiperidermal, up to 4-cm diam., continuous; surface smooth to uneven, grayish- to

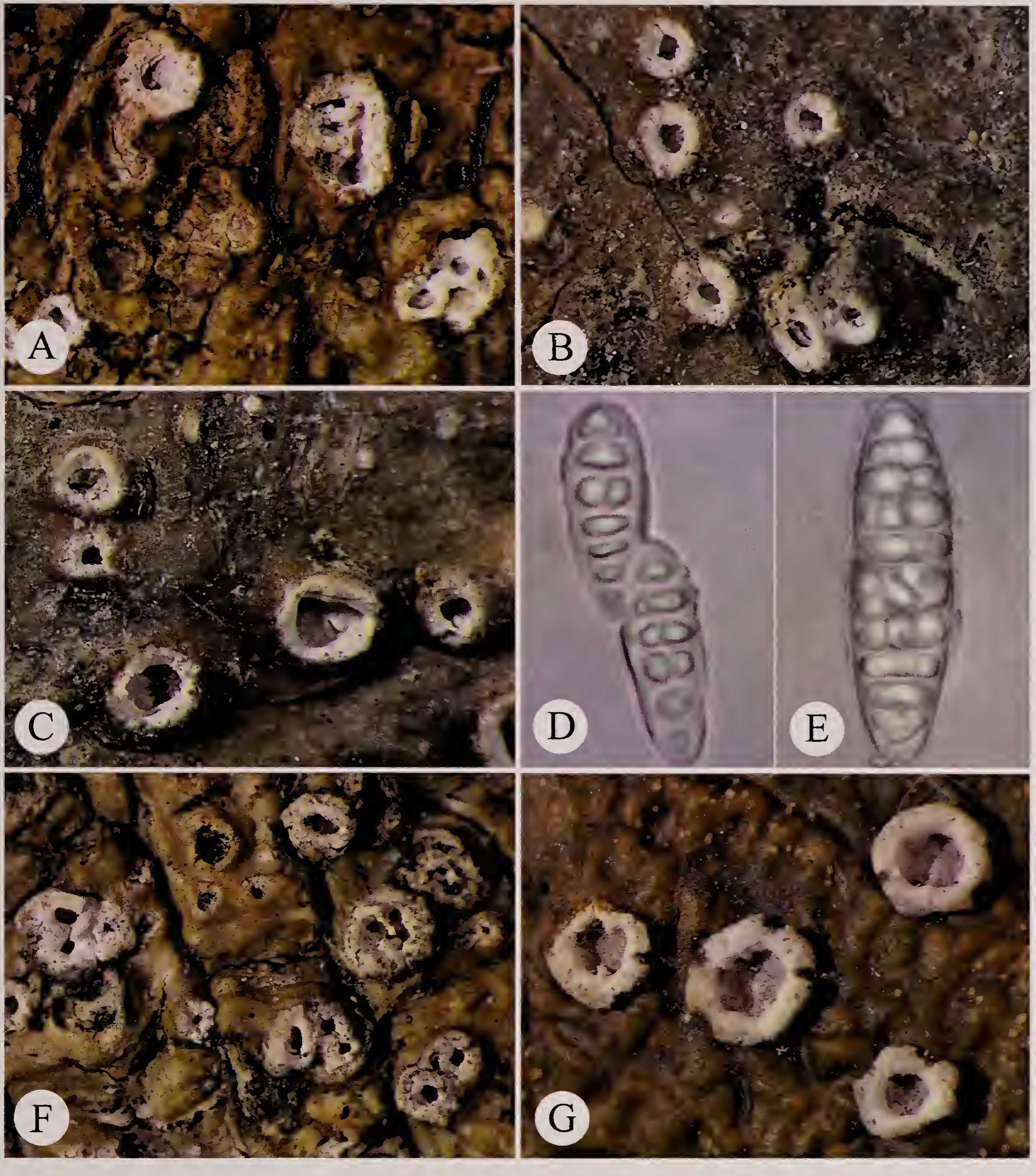

FIG. 5. Morphology and anatomy in Wirthiotremateae. (**A–D**) *Asteristion cupulare* (A: holotype; B–C: Australia, Kalb 19834; D: Australia, NS1610); A–C, thallus with apothecia; D, ascospores. (**E–G**) *A. leucophthalmum* (E: Australia, Tibell 14660; F: Australia, Bailey s.n.; G: Australia, Bailey 278); E, ascospores; F–G, thallus with apothecia.

yellowish-olive; prothallus absent. Thallus in section 100–250 μm thick, cortex cartilaginous, 25–75 μm thick, with irregular photobiont layer, 50–150 μm thick, interspersed with small calcium oxalate crystals, and indistinct epi- to endoperidermal medulla. Photobiont *Trentepohlia*. Ascomata rounded, sometimes aggregate, erumpent to prominent, 0.5- to 1(–2)-mm diam., 0.2–0.4 mm high; disc more or less covered by 0.1- to 0.7(–1.5)-mm-wide pore, flesh-colored, white-pruinose; proper margin indistinct to distinct, entire to fissured, separated from the thalline margin by a narrow split (double margin), forming a white rim around the disc; thalline margin thin, smooth to uneven, lobulate, concolorous with thallus. Excipulum entire, yellow-brown, 20–50 μm wide, paraplectenchymatous, separated from covering thalline layer by a split, the upper portion with a dense layer of gray crystals; columella absent; hypothecium prosoplectenchymatous, 10–20 μm high, hyaline; hymenium 50–70 μm high, hyaline, clear; epithecium 5–10 μm high, gray and granular. Paraphyses unbranched, apically smooth; periphysoids present; asci fusiform, 40–50 × 5–10 μm. Ascospores 6–8 per ascus, ellipsoid, muriform, tapering at one end, with 7–15 transverse septa and 1–3 longitudinal septa per segment, 30–60 × 10–15 μm, 3–4 times long as wide, hyaline, subdistoseptate with lens-shaped lumina, I– (not amyloid). Conidiomata not observed. Secondary chemistry stictic and constictic acids (major) and hypostictic, acetylconstictic, and cryptostictic acids (minor to trace); microscopic section with K+ yellow efflux.

Illustration—Sethy et al. (1987). Page 197, figure 9: Photograph of fertile thallus.

Etymology—The epithet refers to the distinctive white ascomata found in this species.

Distribution and Ecology—*Asteristion leucophthalmum* appears to be a widespread paleotropical species, reported from the Andaman Islands in the Indian Ocean (Sethy et al., 1987), Australia (Mangold et al., 2009), New Caledonia (the holotype), and Oceania (the holotype of var. *annulare*). It is restricted to lowland rain forest.

Discussion—*Asteristion leucophthalmum* is most similar to *A. cupulare* and can be distinguished from that species on the basis of its larger, distinctly muriform ascospores (30–60 μm long versus 15–30 μm long). Like *A. cupulare*, *A. leucophthalmum* is separated from *Thelotrema thesaurum* by the much smaller ascospores and a broad pore. *Thelotrema cyphelloides* Müll. Arg., Bulletin de l'Herbier Boissier 3: 314 (1895) lacks a cortex and has immersed apothecia. *Thelotrema leucophthalmum* var. *annulare* is a new synonym of *A. leucophthalmum*; another variety, *T. leucophthalmum* var. *laceratum*, is a synonym of *Gintarasia megalophthalma* (Müll. Arg.) Kraichak, Lücking & Lumbsch.

Specimens Examined—**AUSTRALIA.** The lectotype and isolectotype of *Leptotrema albocoronatum*. Queensland, various localities in the eastern part of the state: All specimens cited by Mangold et al. (2009). **NEW CALEDONIA.** The lectotype. **VANUATU.** The holotype of *Thelotrema leucophthalmum* var. *annulare*.

Asteristion platycarpoides (Tuck.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 6A–C

MycoBank #818205

Basionym: *Thelotrema platycarpoides* Tuck., Proc. Amer. Acad. Arts Sci. 6: 270. 1866 (1864); *Phaeotrema platycarpoides* (Tuck.) Müll. Arg., Flora 69: 311. 1886; *Chapsa platycarpoides* (Tuck.) Breuss & Lücking in Lücking et al., Bull. Florida Mus. Nat. Hist. 49(4): 140. 2011. Type: Cuba, Wright s.n. (FH-TUCK!, lectotype fide Hale, 1981: 265 and Frisch 2006: 114; BM!, BRU!, FH-TUCK!, G!, H-NYL 22671!, L!, M!, PC!, UPS!, US!, W!, isolectotypes; Wright: Lich. Cub. 157).

Description—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, yellowish-olive, waxy; prothallus absent. Thallus in section to 300 μm thick, cortex prosoplectenchymatous, 5–25 μm thick, with diffuse endoperidermal photobiont layer containing calcium oxalate crystals, and indistinct medulla. Photobiont *Trentepohlia*. Ascomata immersed, round to angular, occasionally aggregate, 0.5- to 1-mm diam.; disc more or less covered by 0.2- to 0.6-mm-wide pore, brown, white-pruinose; proper margin distinct, lobulate, pale brown and pruinose, separated from the thalline margin by a narrow split (double margin), forming a rim around the disc; thalline margin entire to fissured. Excipulum hyaline, with gray crystals on apical surface, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium 60–100 μm high, hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present; asci fusiform, 50–90 × 7–10 μm. Ascospores 8 per ascus, fusiform, (3–)5-septate, 11–15 × 5–10 μm, 3 times long as wide, brown, distoseptate, I+ faintly amyloid. Conidiomata not observed. Secondary chemistry stictic acid (major) and acetylconstictic and constictic acids (minor); apothecial margins sometimes with lichexanthone. Microscopic section with visible to indistinct K+ yellow efflux; apothecial margins UV+ yellow if lichexanthone present.

Illustrations—Hale (1981). Page 263, figure 9, e: Photograph of fertile thallus (Sri Lankan material). Frisch (2006). Page 117, figure 27: Photograph of type collection with lectotype piece indicated. Mangold et al. (2009). Page 220, figure 48, B: Photograph of ascospores (isolectotype).

Etymology—The epithet refers to the similarity of this species with *Asteristion platycarpum* (see below), sharing the brown, transversely septate ascospores.

Distribution and Ecology—The exact distribution of this species is uncertain as it has been treated as a synonym of *A. platycarpum* by some authors (e.g., Frisch, 2006) or mistaken with the latter species (e.g., Hale, 1981). With certainty it is known from Brazil (Cáceres et al., 2014), Cuba (the type), and the southeastern United States (Florida; Lücking et al., 2011). Reports from Sri Lanka by Hale (1981) refer to *A. platycarpum*, and it is likely that reports from Mexico and Indonesia (Java) are also that species. Judging from the few genuine collections available, *Asteristion platycarpoides* seems to be more common in semi-exposed secondary forest and vegetation.

Discussion—We do not yet have molecular data for this species, but considering its close morphological affinity with *A. platycarpum*, we place this species in *Asteristion*. *Asteristion platycarpum* has larger apothecia with a distinctly recurved, chroodiscoid margin always lacking lichexanthone, and its ascospores are predominantly 3-septate and narrower. *Asteristion albo-olivaceum* is morphologically similar but has hyaline, strongly amyloid ascospores. Hale (1981) gave apothecial size as the only difference between *A. platycarpoides* and *A. platycarpum*, but apparently mistook younger specimens of the latter for *A. platycarpoides*. The genuine differences between the two species were discussed by Lücking et al. (2011).

Exsiccati—Lichenes Insulae Cubae, No. 157 (the lectotype and isolectotypes).

Specimens Examined—**USA.** Florida, Collier County, Fakahatchee Strand Preserve State Park, specimens cited by Lücking et al. (2011). **CUBA.** The lectotype and isolectotypes.

Asteristion platycarpum (Tuck.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 6D–F

MycoBank #818206

Basionym: *Thelotrema platycarpum* Tuck., Proc. Amer. Acad. Arts Sci. 5: 406. 1862 (1860); *Phaeotrema platycarpum* (Tuck.) Zahlbr., Cat. Lich. Univers. 2: 609. 1923 (1924); *Chapsa platycarpa* (Tuck.) Frisch, Bibl. Lichenol. 92: 113. 2006. Type: Cuba, Wright s.n. (FH-TUCK! holotype; BM!, BRU!, H-NYL 22667!, G!, L!, M!, PC!, UPS!, US!, W!, isotypes; Wright: Lich. Cub. 139).

Asteristion erumpens Leight., Trans. Linn. Soc. London 27: 163. 1870 (1869); *Phaeotrema erumpens* (Leight.) R. Sant., Symb. Bot. Upsal. 12(1): 423. 1952. Type: Sri Lanka, Thwaites 5 (BM!, lectotype fide Hale, 1981: 265; H-NYL 22683!, S!, UPS!, isolectotypes).

Platygrapha bivela Berk. & Broome, J. Linn. Soc. London, Bot. 14: 109. 1875 (1874). *Cryptodiscus bivelus* (Berk. & Broome) Sacc., Syll. fung. (Abellini) 8: 674. 1889. Type: Sri Lanka, Thwaites 634 (BM!, lectotype fide Hale, 1981: 265).

Platygrapha alborufa Berk. & Broome, J. Linn. Soc. London, Bot. 14: 110. 1875 (1874); *Cryptodiscus alborufus* (Berk. & Broome) Sacc.,

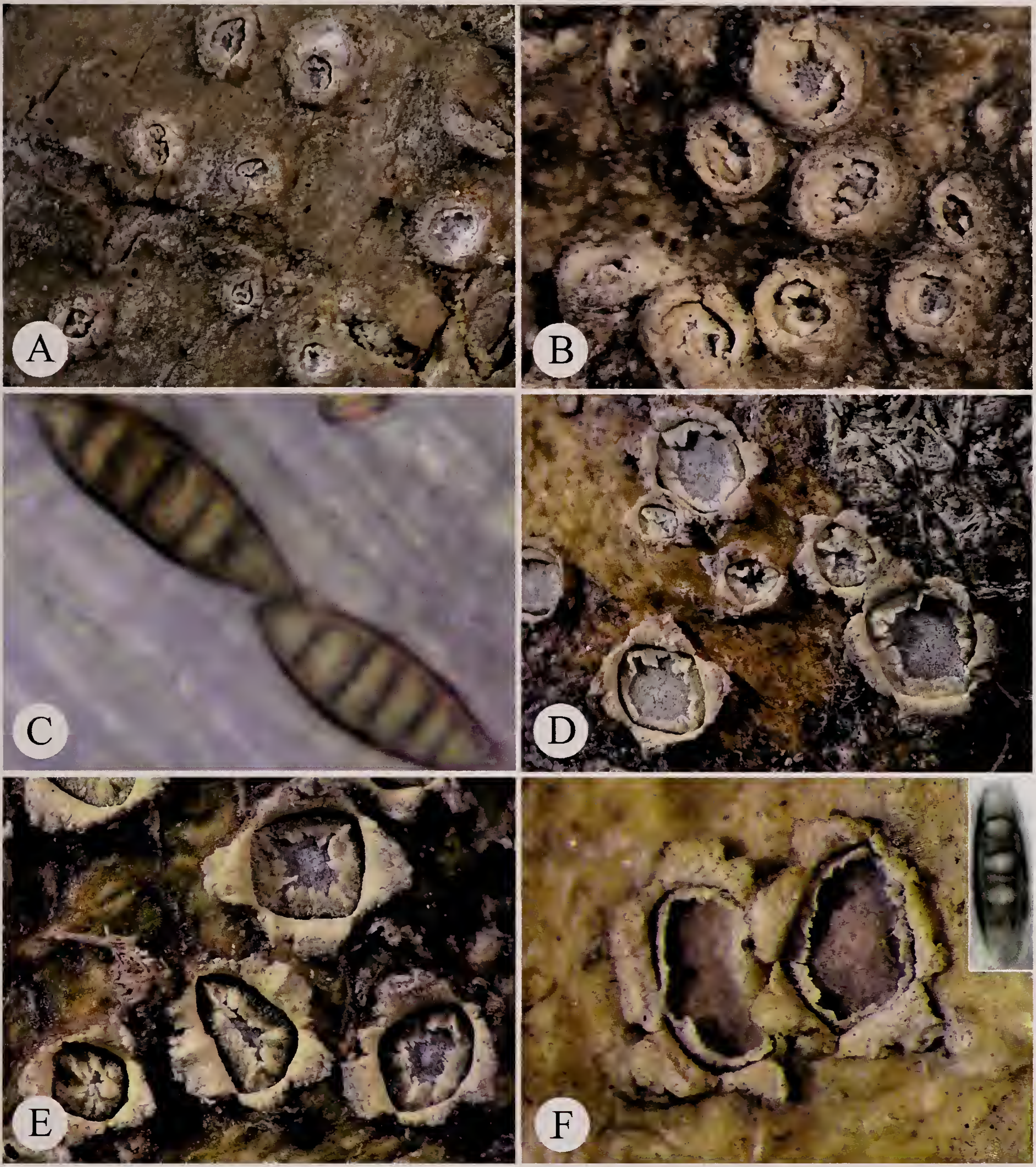

FIG. 6. Morphology and anatomy in Wirthiotremateae. (**A–C**) *Asteristion platycarpoides* (A: Florida, Lücking 26571; B–C: lectotype); A–B, thallus with apothecia; C, ascospores. (**D–F**) *A. platycarpum* (D: Florida, Lücking 26574; E: Florida, Lücking 26757; F: holotype of *Phaeotrema apertum*); D–F, thallus with apothecia; inset in F, ascospore.

Sylloge Fungorum 8: 674. 1889. Type: Sri Lanka, Thwaites 69 (BM!, lectotype fide Hale, 1981: 265).

Phaeotrema apertum C. W. Dodge, Nova Hedwigia, Beih. 12: 98. 1964. Type: Uganda, Dümmer 4293 (BM!, holotype; FH-DODGE!, isotype).

DESCRIPTION—Thallus corticolous, epiperidermal, up to 3-cm diam., continuous; surface smooth to slightly uneven, olive-green to olive-brown; prothallus absent. Thallus in section 70–100 μm thick, with a dense prosoplectenchymatous cortex, 12–25 μm thick, with irregular photobiont layer, 30–70 μm thick, interspersed with clusters of calcium oxalate crystals, grading into irregular and indistinct medulla, epi- to endoperidermal. Photobiont *Trentepohlia*. Ascomata rounded to angular, immersed, 0.5- to 2-mm diam., 0.2–0.3 mm high; disc more or less exposed, partially covered by 0.3- to 1.5-mm-wide pore, dark gray-brown, white-pruinose; proper margin distinct, thin, pale brown and pruinose, fissured to lobulate and strongly erose, separated from the thalline margin by a narrow split (double margin), forming a prominent rim around the disc; thalline margin thin, recurved, covered in yellow pigment on exposed side. Excipulum entire, hyaline to gray-brown, 10–25 μm wide, paraplectenchymatous, separated from covering thalline layer by a split;

columella absent; hypothecium prosoplectenchymatous, 5–10 µm high, hyaline; hymenium 50–65 µm high, hyaline, clear; epithecium 3–10 µm high, gray and granular. Paraphyses unbranched, apically smooth; periphysoids present, 15–25 µm long; asci fusiform, 40–60 × 7–12 µm. Ascospores 8 per ascus, fusiform, 3(–5)-septate, 11–15 × 4–6 µm, 3–4 times long as wide, gray-brown, distoseptate with lens-shaped lumina, I+ faintly amyloid. Conidiomata not observed. Secondary chemistry stictic acid (major) and constictic and acetylconstictic acids (minor); microscopic section with K+ yellow efflux.

Illustrations—Hale (1981). Page 263, figure 9, f: Photograph of fertile thallus (Sri Lankan material). Frisch (2006). Page 39, plate 1, e–f: Scanning electron micrograph and transmitted light micrograph, respectively, of phenocortex (collection from Cameroon). Page 111, plate 6, f: Photograph of *Phaeotrema apertum* (type). Page 116, figure 26: Drawing of ascospores and ascomata cross section. Mangold et al. (2009). Page 220, figure 48, A: Photograph of fertile thallus (Australian material). Sipman et al. (2012). Page 43, figure 9, D: Photograph of fertile thallus (Costa Rican material).

Etymology—The epithet refers to the broad, flat apothecia of this species.

Distribution and Ecology—This species is genuinely pantropical and, apart from the type material from Cuba, Uganda, and Sri Lanka (its synonyms), has been reported from the southeastern United States (Hale, 1981; Lücking et al., 2011), Costa Rica (Sipman et al., 2012), Mexico (Hale, 1981; as *Thelotrema platycarpoides*), Puerto Rico (Salisbury, 1972), Trinidad and Tobago (Salisbury, 1972), Venezuela (Frisch, 2006), Brazil (Frisch, 2006), Cameroon (Frisch, 2006), Sri Lanka (Hale, 1981), Malaysia (Sarawak; Hale, 1981), Indonesia (Java; Hale, 1981), Australia (Mangold et al., 2009), and New Caledonia (Nylander, 1868; Hue, 1891). The reports of *Thelotrema platycarpoides* from Mexico, Sri Lanka, and Indonesia (Java) by Hale (1981) also refer to *A. platycarpum* (see discussion under *A. platycarpoides*). *Asteristion platycarpum* is commonly found in semi-exposed secondary forest and vegetation, as also observed by Hale (1981) in Sri Lanka, which might explain its wide distribution; similar cases are known from the widespread *Dyplolabia azfelii* (Ach.) A. Massal. and *Glyphis cicatricosa* Ach. (Lücking et al., 2014).

Discussion—Within Wirthiotremateae, *Asteristion platycarpum* is unique in its very large apothecia with incurved proper excipulum and recurved, chroodiscoid thalline margin, resembling a flower. It is most similar to *A. platycarpoides*, but that species has smaller apothecia with a more or less entire thalline margin and produces predominantly 5-septate ascospores. The distinct double margin separates this species from otherwise similar taxa in the genera *Astrochapsa* and *Nitidochapsa* (Mangold et al., 2009; Parnmen et al., 2012, 2013; Poengsungnoen et al., 2014). *Nitidochapsa leprieurii* (Mont.) Parnmen, Lücking & Lumbsch, Bryologist 116: 129 (2013) shares the brown, 3-septate ascospores and large apothecia with *A. platycarpum*, but features a fused excipulum with a fluffy surface, a brown rather than olive-green thallus, and lacks secondary substances.

Exsiccati—Lichenes Insulae Cubae, No. 139 (the holotype and isotypes).

Specimens Examined—**USA.** Florida, Collier County, Fakahatchee Strand Preserve State Park, specimens cited by Lücking et al. (2011). **CUBA.** The holotype and isotypes. **UGANDA.** The holotype and isotype of *Phaeotrema apertum*. **COSTA RICA.** Various localities, specimens cited by Sipman et al. (2012). **SRI LANKA.** The lectotype and isolectotype of *Asteristion erumpens*; the lectotype of *Platygrapha bivela*; the lectotype of *Platygrapha alborufa*; additional specimens cited by Hale (1981). **AUSTRALIA.** Specimens cited by Mangold et al. (2009).

Austrotrema I. Medeiros, Lücking & Lumbsch, gen. nov.

MycoBank #818207

A new genus in the family Graphidaceae characterized by small, pore-like apothecia with double margin, I– to I+ faintly amyloid ascospores, and stictic acid chemistry. Type species: *Austrotrema bicinctulum* (Nyl.) I. Medeiros, Lücking & Lumbsch (≡ *Thelotrema bicinctulum* Nyl.).

Description—Thallus corticolous, epiperidermal, continuous; prothallus absent. Cortex prosoplectenchymatous, with irregular to thick photobiont layer interspersed with irregular clusters of calcium oxalate crystals, and indistinct medulla, epi- to endoperidermal. Photobiont *Trentepohlia*. Ascomata minute, immersed to barely erumpent, round; disc almost entirely covered by narrow pore, light to dark gray, white-pruinose; proper margin distinct, slightly to deeply fissured, separated from the thalline margin by a narrow split (double margin), forming a pale rim around the disc; thalline margin thin, smooth, yellow- to olive-brown, entire to slightly eroded or fissured. Excipulum paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium hyaline, clear; epithecium gray and granular. Paraphyses unbranched, apically smooth; periphysoids present to indistinct; asci fusiform. Ascospores 8 per ascus, ellipsoid but tapering at one end, hyaline, transversely septate to (sub-)muriform, distoseptate with lens-shaped lumina, I– to faintly I+. Conidiomata not observed. Secondary chemistry stictic acid (major) with a variety of satellite substances as minor or trace substances.

Etymology—The generic name refers to the occurrence of the type species in the Australian–Southeast Asian region.

Discussion—This new genus resembles certain species of *Thelotrema* with small, immersed-erumpent ascomata and with certainty can only be distinguished at genus level from *Thelotrema* based on molecular phylogenetic data. At the species level, however, *Austrotrema* is distinguished from similar species in *Thelotrema* with transversely septate or small muriform ascospores and stictic acid, such as *T. infundibularis* Tat. Matsumoto, Journal of the Hattori Botanical Laboratory 88: 26 (2000) and *T. capetribulense* Mangold in Lumbsch et al., Australian Systematic Botany 21: 221 (2008), by the presence of a dense, prosoplectenchymatous cortex, a feature rarely found in genuine *Thelotrema* species (Rivas Plata et al., 2010b). *Austrotrema* can also be confused with species of *Leucodecton*; however, the only species with hyaline ascospores and lepadinoid apothecia (with double margin) previously placed in that genus, *L. expallescens* (Nyl.) Rivas Plata & Lücking and *L. peninsulae* (R. C. Harris) Rivas Plata & Lücking, have now been shown to be closely related to *Nadvornikia hawaiiensis* (see below), thus belonging in the same tribe as *Austrotrema*. Within Wirthiotremateae, *Austrotrema* can be distinguished from *Asteristion* by the small ascomata with entire, pore-like thalline margin and from *Wirthiotrema* by the less glossy thallus which is not splitting internally. Species of *Wirthiotrema* also tend to have a more greenish thallus, while the thalli of *Austrotrema* species are brownish. *Nadvornikia expallescens* differs in its pale gray thallus with more or less loose

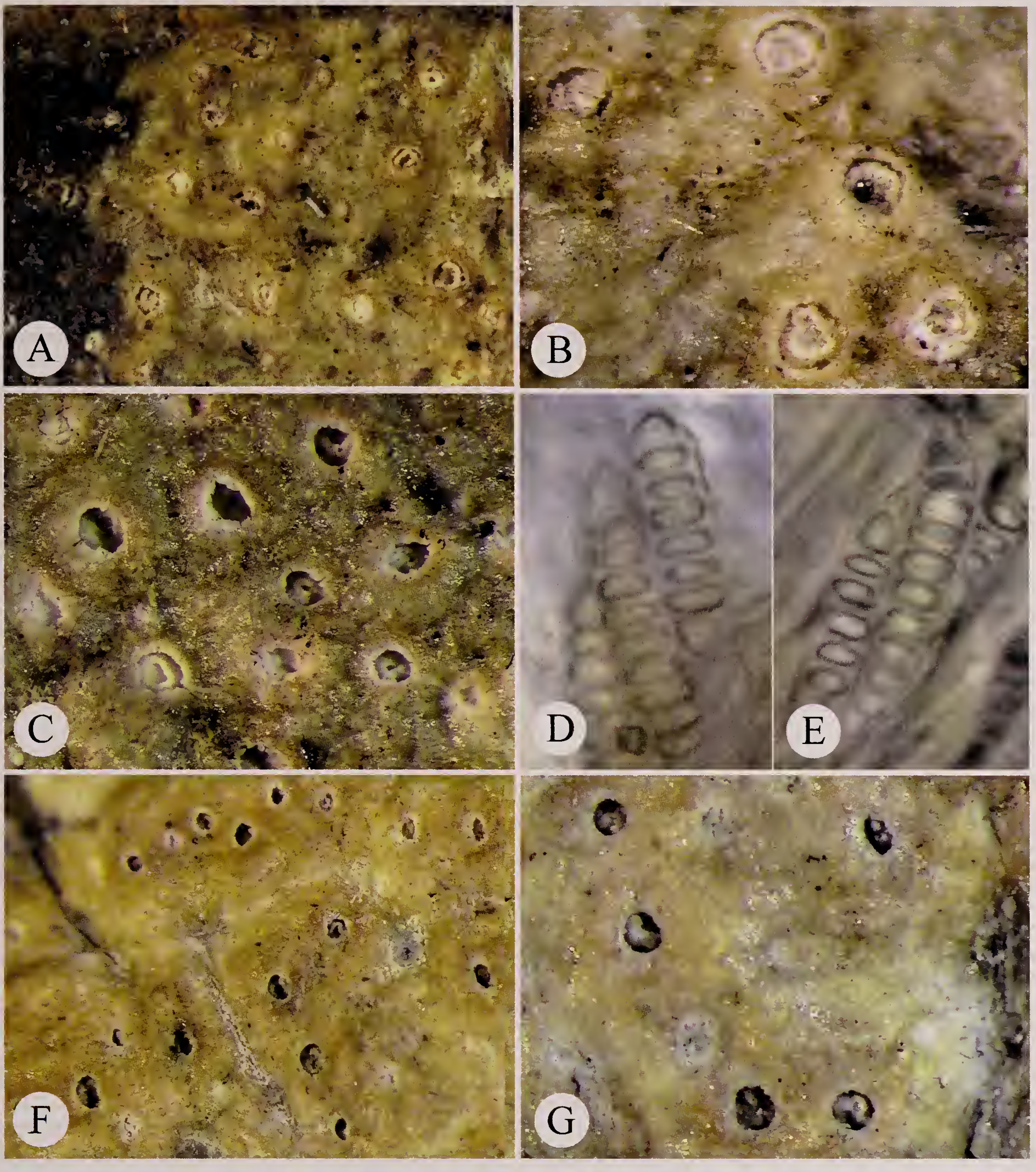

Fig. 7. Morphology and anatomy in Wirthiotremateae. (**A–D**) *Austrotrema bicinctulum* (lectotype); A–C, thallus with apothecia; D, ascospores. (**E–G**) *A. terebrans* (E, G: holotype; F: isotype in UPS). E, ascospores; F–G, thallus with apothecia.

cortex and the prosoplectenchymatous excipulum which is visible as a distinct white rim around the disc. As circumscribed here, the genus *Austrotrema* contains three species.

KEY TO SPECIES

1A. Ascospores muriform . . . . **A. myriocarpum**
1B. Ascospores transversely septate 2
  2A. Periphysoids indistinct; surface smooth to uneven . . . . **A. bicinctulum**
  2B. Periphysoids rather distinct; surface uneven to verrucose . . . . **A. terebrans**

Austrotrema bicinctulum (Nyl.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 7A–D

MycoBank #818208

Basionym: *Thelotrema bicinctulum* Nyl., Ann. Sci. Nat., Bot., Sér. 4, 15: 46. 1861; *Ocellularia bicinctula* (Nyl.) Müll. Arg., Mém. Soc. Phys. Hist. nat. Genève 29(8): 9. 1887b. Type: New Caledonia, Pancher s.n. (H-NYL 22804a!, lectotype fide Frisch, 2006: 282).

Ascidium octoloculare C. Knight in Bailey, Proc. R. Soc. Qd. 1: 152. 1884; *Porina octolocularis* (C. Knight) C. Knight in Shirley, Proc. R.

Soc. Qd. 6: 188. 1889; *Ocellularia octolocularis* (C. Knight) Shirley, Proc. R. Soc. Qd. 6: 188. 1899. Type: Australia (Queensland), Bailey 204 (WELT!, lectotype fide Mangold et al., 2009: 657; BRI!, isolectotypes).

Description—Thallus corticolous, epiperidermal, up to 4-cm diam., continuous; surface uneven, olive- to yellow-brown; prothallus absent. Thallus in section 60–110 µm thick, cortex dense, prosoplectenchymatous, 25–40 µm thick, with irregular photobiont layer, 10–30(–100) µm thick, interspersed with irregular clusters of large (20–40 µm) calcium oxalate crystals, and indistinct medulla, epi- to endoperidermal. Photobiont *Trentepohlia*. Ascomata minute, immersed to barely erumpent, round, 0.1- to 0.35-mm diam., 0.1–0.2 mm high; disc barely visible, almost entirely covered by 0.05- to 0.1-mm-wide pore, light to dark gray, white-pruinose; proper margin distinct, slightly to deeply fissured, separated from the thalline margin by a narrow split (double margin), forming a white to pale brown rim around the disc; thalline margin thin, smooth, yellow- to olive-brown, entire to slightly eroded or fissured. Excipulum split apically, pale yellow-brown, 10–20 µm wide, paraplectenchymatous, separated from covering thalline layer by a split; laterally covered by algiferous thallus, 25–70 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–20 µm high, hyaline; hymenium 75–100 µm high, hyaline, clear; epithecium 3–10 µm high, gray and granular. Paraphyses unbranched, apically smooth; periphysoids indistinct; asci fusiform, 50–70 × 10–12 µm. Ascospores 8 per ascus, ellipsoid but tapering at one end, 5–9-septate, 15–30 × 5–7 µm, 3–5 times long as wide, hyaline, distoseptate with lens-shaped lumina, I– (non-amyloid) to I+ faintly amyloid. Conidiomata not observed. Secondary chemistry stictic acid (major); constictic, hypostictic, acetylconstictic, or hypoconstictic acids may be present as minor to trace satellite substances. Microscopic section with visible to indistinct K+ yellow efflux.

Illustrations—Frisch (2006). Page 286, figure 89: Drawing of ascospores and ascomata cross section. Page 287, figure 90: Sketch of type specimen with lectotype piece indicated. Page 293, plate 15, b: Photograph. Mangold et al. (2009). Page 362, figure 117: Photographs of fertile thallus (Australian collection) and cross section of ascomata (lectotype).

Etymology—The epithet refers to the appearance of the apothecia, in which the discs are encircled (Latin: cinctus = encircled, girdled, or enclosed) by two layers (the thalline margin and the proper margin).

Distribution and Ecology—This species is with certainty known only from Australasia. Reports from Africa (Frisch, 2006) refer to *A. terebrans* (see below). According to Mangold et al. (2009), the species is found in lowland rain forest, coastal forest, and mangroves, indicating a tolerance for semi-exposed microhabitats.

Discussion—Molecular data showed that what had initially been identified as *Austrotrema bicinctulum* (Rivas Plata et al., 2013) actually consisted of two phylogenetically distinct taxa. Australian material represent *A. bicinctulum* s.s., while a single specimen from Thailand was positioned outside that the core group. This specimen corresponds morphologically to the type material of *Thelotrema terebrans*, which therefore is here reinstated as a separate species within *Austrotrema* (see below). *Austrotrema bicinctulum* can be distinguished from *A. terebrans* on the basis of its less distinct periphysoids, less distinctly amyloid ascospores, and smooth to uneven thallus surface. *Austrotrema bicinctulum* bears some resemblance to *Leucodecton subcompunctum* (Nyl.) Frisch, Bibliotheca Lichenologica 92: 162 (2006), which has brown, muriform ascospores.

Bailey and James (1975) stated that *Thelotrema bicinctulum* had been confused with Australasian material of *T. subtile* Tuck. The latter is now recognized as a distinct taxon, described under the name *T. pseudosubtile* Mangold (Lumbsch et al., 2008), but with the earlier name *T. jugale* (Müll. Arg.) Lücking in Sipman et al., Phytotaxa 55: 195 (2012) taking priority (Sipman et al., 2012). *Thelotrema jugale* differs from *Austrotrema bicinctulum* in the whitish thallus and larger, strongly amyloid ascospores, as well as in the lack of secondary substances. Mangold et al. (2009) listed *Ocellularia demersa* Müll. Arg. as a synonym of *T. bicinctulum*, but that species is now being recognized as a separate taxon in *Thelotrema* s.s. (Sipman et al., 2012): *Thelotrema demersum* (Müll. Arg.) G. Salisb., Nova Hedwigia 29: 408 (1978). This species differs from *A. bicinctulum* in its irregular, loose to compacted cortex and slightly larger (7–11-septate, 20–30 × 5–7 µm), fully amyloid ascospores.

Specimens Examined—**NEW CALEDONIA**. The lectotype. **AUSTRALIA**. Queensland. Daintree National Park, Mangold 32c (F), Mangold 34f (F). The lectotype and isolectotypes of *Ascidium octoloculare*; additional specimens cited by Mangold et al. (2009).

***Austrotrema myriocarpum* (Fée) I. Medeiros, Lücking & Lumbsch, comb. nov.**

Figure 7D

MycoBank #818210

Basionym: *Thelotrema myriocarpum* Fée, Essai Cryptog. Écorc. 94. 1825. Type: South America, s.col. (PC!, lectotype fide Hale, 1978: 45; H-NYL, L, isolectotypes).

Description—Thallus corticolous, epiperidermal, up to 5-cm diam., continuous; surface uneven, olive- to yellow-brown; prothallus absent. Thallus in section 70–120 µm thick, cortex dense, prosoplectenchymatous, 25–30 µm thick, with irregular photobiont layer, 30–70 µm thick, interspersed with irregular clusters of large (20–40 µm) calcium oxalate crystals, and indistinct medulla, epi- to endoperidermal. Photobiont *Trentepohlia*. Ascomata immersed to erumpent, round, 0.25- to 0.35-mm diam., 0.1–0.2 mm high; disc covered by 0.15- to 0.25-mm-wide pore, light to dark gray, white-pruinose; proper margin distinct, slightly fissured, separated from the thalline margin by a narrow split (double margin), forming a white to pale brown rim around the disc; thalline margin thin, smooth, yellow- to olive-brown, entire to slightly eroded. Excipulum split apically, gray-brown, 10–20 µm wide, paraplectenchymatous, separated from covering thalline layer by a split; laterally covered by algiferous thallus, 30–80 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–20 µm high, hyaline; hymenium 100–120 µm high, hyaline, clear; epithecium 5–10 µm high, gray and granular. Paraphyses unbranched, apically smooth; periphysoids indistinct; asci fusiform, 80–100 × 12–15 µm. Ascospores 8 per ascus, ellipsoid to fusiform, muriform with 9–13 transverse and 1–3 longitudinal septa per segment, 30–50 × 8–12 µm, 3.5–4.5 times long as wide, hyaline, distoseptate with lens-shaped to rounded lumina, I– (non-amyloid) to I+ faintly amyloid. Conidiomata not observed. Secondary chemistry stictic acid (major); constictic, hypostictic, acetylconstictic, or hypoconstictic acids may be present as minor to trace satellite substances. Microscopic section with visible to indistinct K+ yellow efflux.

Illustrations—Hale (1978). Page 6, figure 2, h: Thallus photograph of lectotype. Page 46, figure 13, b: Photograph of fertile thallus. Mangold et al. (2009). Page 384, figure 132: Photographs of fertile thallus and ascospores (Australian collections).

Etymology—The epithet refers to the numerous small apothecia (Greek: myrio- = numerous; carpos = fruits).

Distribution and Ecology—*Austrotrema myriocarpum* appears to be a neotropical species, known from the type from South America, possibly Venezuela according to Hale (1978). We have not checked the material reported by Hale (1978) from Panama (also cited by Sipman et al., 2012), which according to the small ascospores could represent *Thelotrema submyriocarpum* Lücking in Sipman et al., Phytotaxa 55: 193 (2012), a species likely to belong in *Thelotrema* s.s. due to its distinct periphysoids (Sipman et al., 2012). The material reported from Australia as *T. myriocarpum* (Mangold et al., 2009) belongs in *Wirthiotrema duplomarginatum* (see below).

Discussion—*Thelotrema myriocarpum* is here included in *Austrotrema* based on the striking similarities with *A. bicinctulum* in thallus and apothecial morphology and anatomy, including the distoseptate but non-amyloid to faintly amyloid ascospores. Notably, in the key to *Thelotrema* by Rivas Plata et al. (2010b), species with small, muriform ascospores, stictic acid chemistry, and dense cortex formerly placed in that genus, viz. *T. myriocarpum*, *T. cupulare*, *T. alboannuliforme*, and *T. albo-olivaceum*, are now all included in tribe Wirthiotremateae, in the genera *Austrotrema* and *Asteristion*, suggesting that this combination of characters is largely diagnostic for Wirthiotremateae.

Specimens Examined—**SOUTH AMERICA (VENEZUELA?).** The lectotype and isolectotypes. **BRAZIL**. Amapa, Cáceres & Aptroot 27220 (ise).

Austrotrema terebrans (Nyl.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 7E–G

MycoBank #818211

Basionym: *Thelotrema terebrans* Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 7: 166. 1873; *Ocellularia terebrans* (Nyl.) Zahlbr., Cat. Lich. Univers. 2: 602. 1923; *Myriotrema terebrans* (Nyl.) Hale, Mycotaxon 11: 135. 1980. Type: India (Andaman Islands), Kurz 80 (h-nyl 22771!, lectotype fide Hale, 1981: 294; ups!, isolectotype).

Description—Thallus corticolous, epiperidermal, up to 5-cm diam., continuous; surface uneven to verrucose, greenish-brown; prothallus absent. Thallus in section 120–200 μm thick, cortex prosoplectenchymatous, 10–30 μm thick, with thick photobiont layer, 100–140 μm thick, interspersed with large (20–40 μm) irregular clusters of calcium oxalate crystals, and indistinct medulla, epi- to endoperidermal. Photobiont *Trentepohlia*. Ascomata minute, immersed to barely erumpent, 0.1- to 0.3(−0.6)-mm diam., 0.2–0.4 mm high; disc largely concealed by proper margin and 0.05- to 0.1-mm-wide pore, gray-brown, white-pruinose; proper margin distinct, slightly fissured, separated from the thalline margin by a narrow split (double margin), forming a whitish rim around the disc; thalline margin thick, smooth, concolorous with thallus, pore margin entire to slightly fissured. Excipulum entire, yellow-brown becoming darker brown above, 15–30 μm wide, paraplectenchymatous, separated from covering thalline layer by a split; laterally covered by algiferous thallus, 100–150 μm thick; columella absent; hypothecium prosoplectenchymatous, 20–25 μm high, light yellow-brown; hymenium 80–110 μm high, hyaline, clear; epithecium 10–15 μm high, gray and granular. Paraphyses unbranched, apically smooth; periphysoids present, especially towards upper portion of apothecium; asci fusiform, 75–105 × 4–12 μm. Ascospores 8 per ascus, ellipsoid with one end tapering, 6–8-septate, 20–30 × 5–7 μm, 3–5 times long as wide, hyaline, distoseptate with lens-shaped lumina, I+ faintly amyloid. Conidiomata not observed. Secondary chemistry stictic acid (major) and hypostictic and constictic acids (minor); microscopic section with visible K+ yellow efflux.

Etymology—The epithet is derived from the Latin terebrare ("bore through") and refers to the minute apothecial pores which look like little holes bored in the thallus.

Distribution and Ecology—This species is known from the paleotropics, including Cameroon (Frisch, 2006; as *T. bicinctulum*), India (the type material), and Thailand (the specimen sequenced here). According to Frisch (2006; as *T. bicinctulum*), in Cameroon this taxon grows on trees in dry and exposed sites, such as along the seashore.

Discussion—*Thelotrema terebrans* was synonymized with *T. bicinctulum* by Mangold et al. (2009). Our molecular data showed that material previously identified as *T. bicinctulum* (Rivas Plata et al., 2013) fell into two clades, one of which corresponds morphologically to the type of *T. terebrans*. Thus, both are here recognized as separate species within *Austrotrema*. *Austrotrema terebrans* differs from *A. bicinctulum* mainly in its uneven to verrucose thallus surface, the more distinct periphysoids, and the persistently though weakly amyloid ascospores. Also, the distribution is different, although thus far only few collections are available, suggesting an African–Asian range for *A. terebrans* and an Australasian range for *A. bicinctulum*.

Specimens Examined—**CAMEROON**. South Province, Kribi, Bwambe Village, specimen cited by Frisch (2006) in hb. Kalb. **INDIA**. Andaman Islands: The lectotype and isolectotype. **THAILAND**: Lumbsch 20206b (f).

Nadvornikia Tibell

MycoBank #25652

Nadvornikia Tibell, Beih. Nova Hedwigia 79: 672. 1984 [replacement name]; *Stephanophoron* Nádv., Ann. Mycol. 40: 136. 1942 [nom. illeg.; non *Stephanophorus* Flot.]. Type species: *Nadvornikia hawaiiensis* (Tuck.) Tibell.

Description—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven; prothallus absent. Cortex absent to loose and irregular, with photobiont layer interspersed with calcium oxalate crystals, and endoperidermal medulla. Vegetative propagules absent or soredia present. Photobiont *Trentepohlia*. Ascomata rounded, immersed to sessile, mazaediate or not; proper margin entire to fissured; thalline margin entire. Excipulum entire, prosoplectenchymatous; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium hyaline, clear; epithecium thin to indistinct. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform. Ascospores 8 per ascus, 1-septate to submuriform, hyaline or dark brown, distoseptate, I− (not amyloid). Conidiomata not observed. Secondary chemistry stictic acid and satellite substances.

Etymology—The generic name *Nadvornikia* honors the Czech lichenologist Josef Nádvorník (1906–1977), who first considered the type species of the genus to represent a separate generic lineage.

Discussion—The ambiguity of the above description and the separation of *Nadvornikia* into two parts in the key highlight the fact that *Nadvornikia* as emended here is morphologically heterogeneous, despite comprising only four species. The previous concept of *Nadvornikia* included only the two mazaediate species *N. hawaiiensis* and *N. sorediata*. Our molecular data now suggest that the genus concept should be expanded to include two other species, *N. expallescens* and *N. peninsulae*, formerly placed in *Thelotrema*, *Myriotrema*, or *Leucodecton*. This is somewhat counterintuitive, considering how distinctive the two mazaediate species are among the thelotremoid Graphidaceae: *Schistophoron* Stirt. is the only other genus in Graphidaceae with mazaediate ascomata, and species of that genus possess lirellae (Tehler et al., 2009). Yet the dismantling of Caliciales (Tibell, 1984; Prieto et al., 2013) has shown that mazaedia eveloved several times independently within the Ascomycota as an ecological adaptation and hence are of weak systematic importance. For instance, the mazaediate genus *Heterocyphelium* has been shown to be closely related to the non-mazaediate genus *Alyxoria* in Arthoniales (van den Broeck et al., in prep.). Indeed, *Nadvornikia* itself was, as a mazaediate genus, once included in Caliciales, and it was only recently that it was definitively shown to belong to (the former) Thelotremataceae (Lumbsch et al., 2004). In the case of *Nadvornikia*, the paraphyletic position of the non-mazaediate taxa relative to the mazaediate species requires the expansion of *Nadvornikia* to include both non-mazaediate taxa, as otherwise one would have to establish two separate, new genera for each of these two species. Notably, all four species in this genus share a prosoplectenchymatous excipulum, a trait found nowhere else in Wirthiotremateae.The name *Stephanophoron* provides an interesting nomenclatural problem.

The name was established by Nádvorník (1942) for *Acolium hawaiiense* but had already been used by Nylander (1900) for two species of *Leptogium*. Nylander's name, however, is not a newly introduced generic name but an invalid orthographic variant of the name *Stephanophorus* Flot. (Flotow, 1843). For the consideration of homonymy, the name *Stephanophoron* Nyl. hence has no bearing and thus *Stephanophoron* Nádv. would be legitimate, since according to ICN Art. 53.3 Example 12, the two names *Stephanophorus* and *Stephanophoron* would not be considered as likely to be confused [see cited example *Peltophorus* Desv. and *Peltophorum* (Vogel) Benth.]. However, ICN Art. 53.3 also states: "If established practice has been to treat two similar names as homonyms, this practice is to be continued if it is in the interest of nomenclatural stability" (McNeill et al, 2012: 117). Thus, the replacement of the name *Stephanophoron* Nádv. by *Nadvornikia* Tibell is to be followed.

Distinction of Mazaediate *Nadvornikia* from Similar Taxa—A number of other mazaediate taxa resemble the mazaediate *Nadvornikia* species; a key to these genera has been published previously (Tibell, 1996) and since then no further genera have been added, the key is not repeated here, but a short discussion on the diagnostic characters follows. There are three lichenized mazaediate genera with crustose thalli, sessile ascomata with thalline margin, and 1-septate ascospores: *Nadvornikia*, *Pyrgillus* (Pyrenulaceae), and *Tylophoron* (Arthoniaceae). *Tylophoron* forms rather narrow ascomata with a basal thalline margin not visible from above; hence, the ascomata from above appear black (resembling cigarettes); the thallus and/or the ascomata margin may contain lecanoric acid (C+ red). Both *Pyrgillus* and *Nadvornikia* have a white rim on the ascomata when seen from above, but the ascomata in *Pyrgillus* are laterally black, with the white rim partially covered by the mazaedium, whereas in *Nadvornikia* they are covered by thick thallus tissue and therefore appear whitish, and the whitish rim is slightly prominent and often coronate. *Schistophoron*, the only other genus in Graphidaceae with distinctly mazaediate ascomata, has elongate ascomata and 3-septate to submuriform ascospores and is unlikely to be confused with *Nadvornikia* (Tibell, 1996).

Key to Mazaediate Species

1A. Soredia present .... ***N. sorediata***
1B. Soredia lacking .... ***N. hawaiiensis***

Key to Non-Mazaediate Species

1A. Apothecia large, prominent; ascospores fusiform-tapering, ca. 3 times long as wide .... ***N. peninsulae***
1B. Apothecia small, immersed-erumpent; ascospores ellipsoid, ca. 2–2.5 times long as wide ..... ***N. expallescens***

Nadvornikia expallescens (Nyl.) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 8A–B

MycoBank #818213

Basionym: *Thelotrema expallescens* Nyl., Flora 59: 560. 1876; *Leucodecton expallescens* (Nyl.) Rivas Plata & Lücking, Lichenologist 42: 184. 2010b. Type: Cuba, Wright 86 (H-NYL, holotype, not seen; UPS, US!, isotypes).

Description—Thallus corticolous, epiperidermal, up to 6-cm diam., continuous; surface smooth to uneven, pale greenish-gray; prothallus absent. Thallus in section 60–125 µm thick, cortex loose to cartilaginous, 5–20 µm thick, with continuous photobiont layer, 25–75 µm thick, beneath layer of large (ca. 30-µm diam.) calcium oxalate crystals, and indistinct epi- to endoperidermal medulla, 10–30 µm thick. Photobiont *Trentepohlia*. Ascomata rounded, erumpent, 0.2- to 0.3-mm diam., 0.1–0.2 mm high; disc partially visible beneath 0.05- to 0.1-mm-wide pore, flesh- to amber-colored, white-pruinose; proper margin distinct, entire, sometimes separated from the thalline margin by a narrow split (double margin), forming a white rim around the disc; thalline margin thick, smooth, entire to becoming eroded, concolorous with thallus. Excipulum entire, pale yellow-brown, 15–30 µm wide, becoming darker and thicker apically, prosoplectenchymatous, partly separated from covering thalline layer by a split; laterally covered by algiferous thallus, 50–70 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–20 µm high, hyaline; hymenium 80–100 µm high, hyaline, clear; epithecium 5–10 µm high, hyaline. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 85–105 × 6–10 µm. Ascospores 8 per ascus, ellipsoid, submuriform with 3–5 transverse and 0–1 longitudinal septa per segment, 13–17 × 5–8 µm, 2–2.5 times long as wide, hyaline, subdistoseptate, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic acid (major); constictic, hypoconstictic, and hypostictic acids (minor) microscopic section with K+ yellow efflux.

Etymology—Nylander (1900) gave no explanation for choosing the epithet *expallescens*, although it probably refers

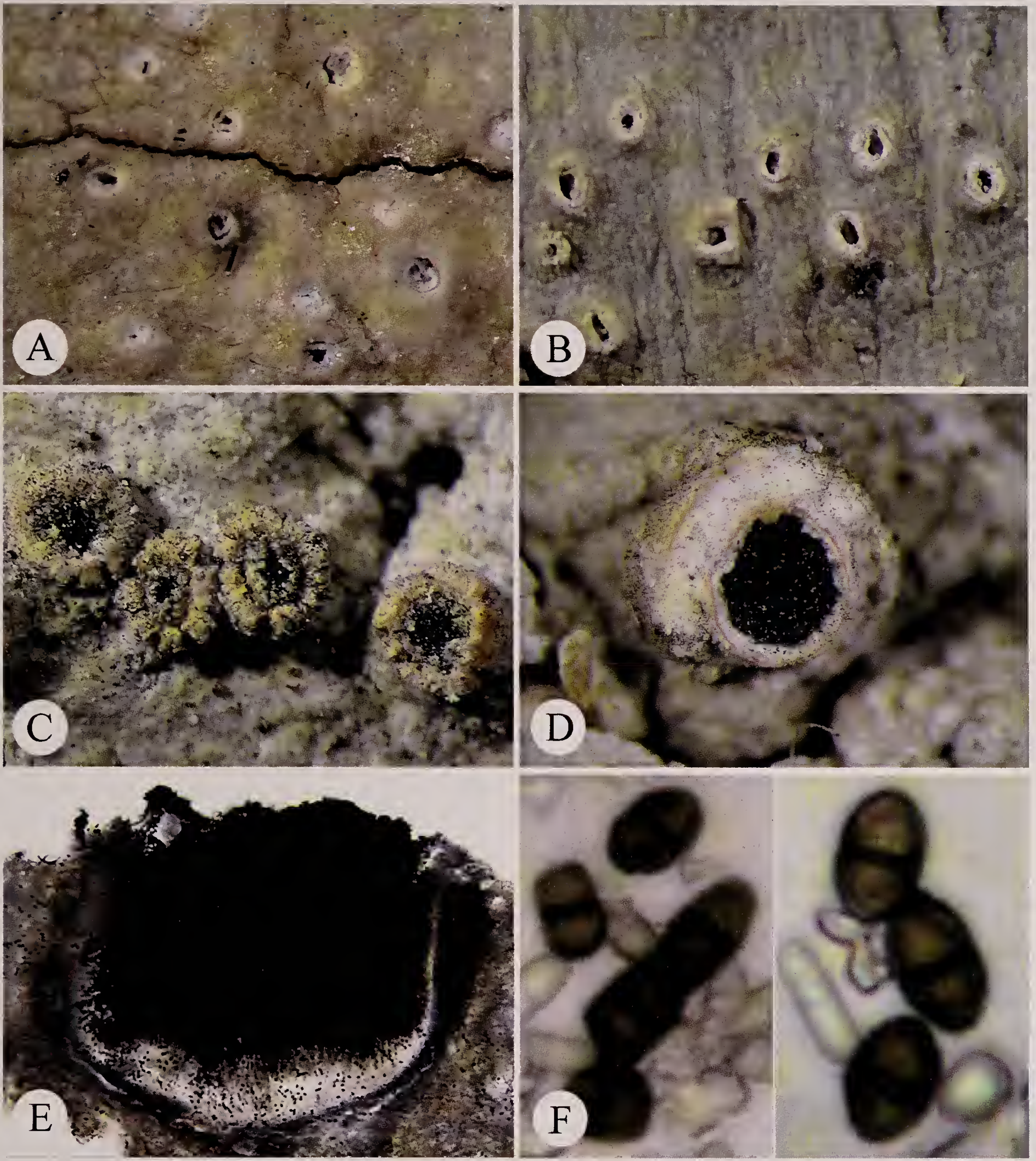

FIG. 8. Morphology and anatomy in Wirthiotremateae. (**A–B**) *Nadvornikia expallescens* (A: isotype in US; B: Costa Rica, Lücking 15069), thallus with apothecia. (**C–F**) *N. hawaiiensis* (C: Costa Rica, Dodge 7826; D–F: Australia, S36b); C–D, thallus with mazaedia; E, mazaedium in transverse section; F, ascospores.

to the rather pale thallus (Latin: expallescere = becoming pale).

DISTRIBUTION AND ECOLOGY—The species is known with certainty only from Cuba and Costa Rica, where the type material was collected. A specimen labeled as originating from the United States in GBIF (UPS L-076178) is actually from Cuba. Occasional reports from other areas in the literature need to be checked, as this species is easily confused with superficially similar taxa in *Austrotrema*, *Leucodecton*, and *Thelotrema*. The Costa Rican material suggests this species is a lower montane rain forest taxon.

DISCUSSION—This species is distinguishable from the other non-mazaediate species of *Nadvornikia*, *N. peninsulae*, on the basis of its much smaller, erumpent ascomata. *Nadvornikia expallescens* is similar in appearance to *Leucodecton inspersum* Rivas Plata & Lücking, Fungal Diversity 58: 24 (2012), which has an inspersed hymenium (clear in *N. expallescens*) and larger ascospores. We considered *L. inspersum* as a potential member of Wirthiotremateae, but sequence data (mtSSU, GenBank KX901735; EF1-α, GenBank KX901707) confirm that it belongs in the Thelotremateae (the tribe which includes *Leucodecton* s.s.).

Exsiccati—Lichenes Insulae Cubae, No. 86 (the holotype and isotypes).

Specimens Examined—**CUBA**. Locality unknown: The isotype. **COSTA RICA**. Puntarenas. Las Tablas Protection Zone, Las Alturas Station, 26 June 2002, Lücking 15069 (CR, F); additional specimens cited by Sipman et al. (2012).

Nadvornikia hawaiiensis (Tuck.) Tibell

Figure 8C–F

MycoBank #107541

Nadvornikia hawaiiensis (Tuck.) Tibell, Beih. Nova Hedwigia 79: 672. 1984; *Acolium hawaiiense* Tuck., Proc. Amer. Acad. Arts Sci. 7: 232. 1868 (1866); *Cyphelium hawaiiense* (Tuck.) Zahlbr., Cat. Lich. Univ. 1: 664. 1922; *Stephanophoron hawaiiense* (Tuck.) Nádv., Ann. Mycol. 40: 136. 1942; *Tylophoron hawaiiense* (Tuck.) H. Magn. in Magnusson and Zahlbruckner, Ark. Botanik 31A (1): 23. 1944. Type: U.S.A. (Hawaii), Oahu, Waialua Mountains, Mann s.n. (UPS!, lectotype fide Mangold et al., 2009: 655).

Tylophoron diplotylium Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 46. 1868; *Nadvornikia diplotylia* (Nyl.) Pant & Awasthi, Biovigyanam 15: 12. 1989. Type: New Caledonia, s.col. D23 (H-NYL 40422, holotype).

Description—Thallus corticolous, epiperidermal, up to 4-cm diam., continuous; surface uneven, often covered with bumps of immature apothecia, whitish to yellowish-gray; prothallus absent. Thallus in section 150–200 μm thick, cortex thin and sparse, 5–10 μm thick when present, surface mostly ecorticate, with irregular photobiont layer, 55–95 μm thick, interspersed with large calcium oxalate crystals (ca. 20- to 40-μm diam.), and endoperidermal medulla, 100–120 μm thick, interspersed with numerous clear crystals (ca. 20-μm diam.). Photobiont *Trentepohlia*. Ascomata rounded, sessile, 0.9- to 1.6-mm diam., 0.3–0.6 mm high; disc not visible under mazaedial mass, pore 0.5- to 1-mm diam.; proper margin indistinct, brown, fissured, rarely separated from the thalline margin; thalline margin thin to thick, entire to eroding, white to pale gray. Excipulum entire, hyaline to yellow-brown, 25–45 μm wide, prosoplectenchymatous; columella absent; hypothecium prosoplectenchymatous, 30–50 μm high, hyaline to very pale brown; hymenium 200–400 μm high, hyaline but difficult to view due to mazaedium, clear; epithecium not visible due to mazaedial mass. Paraphyses unbranched, apically smooth; periphysoids absent; asci linear to fusiform, 50–100 × 5–8 μm, disintegrating at maturity and releasing ascospores into mazaedial mass. Ascospores 8 per ascus, ellipsoid, with one end rounded and the other sometimes, but not always, acute, 1-septate, 4–9 × 3–6 μm, 1–2 times long as wide, dark olive-brown, appearing black en masse, distoseptate, minutely ornamented, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic (major) and constictic (minor) acids; microscopic section with K+ yellow efflux.

Illustrations—Lumbsch et al. (2004). Page 11, figure 1, A, C, E–F: Thallus, ascomata cross section, ascus, and ascospore photographs. Sipman et al. (2012). Page 105, figure 19, F–H: Photographs of fertile thallus (Costa Rican material).

Etymology—The epithet refers to the Hawaiian islands, the type locality of this species.

Distribution and Ecology—This species appears to have a pantropical distribution (Harris, 1990; Mangold et al., 2009), possibly explained by both its passive ascospore dispersal through mazaedia and its preference of semi-exposed microsites, often on decomposing bark of old, exposed trees. It has been reported from Australia (Mangold et al., 2009), Bermuda (Berger and LaGreca, 2014), Brazil (Tibell, 1996), Cuba (Tibell, 1996), Hawaii (the type), Mexico (Tibell, 1996), New Caledonia (Elix & McCarthy, 2008), and the mainland United States (Florida; Harris, 1990). Apart from the fact that the dry ascospore mass produced in the mazaedia are easily dispersed by wind, Tibell (1994) suggests that the ornamented ascospores may help adhere them to animal dispersal agents and facilitate the simultaneous dispersal of multiple ascospores over long distances. A neotropical distribution map is available in Tibell (1996).

Discussion—Due to the conspicuous, mazaediate ascomata, *Nadvornikia hawaiiensis* is not likely to be mistaken for any other species within Wirthiotremateae, except *N. sorediata*. These two species can be distinguished based on the presence or absence of soredia. *Nadvornikia hawaiiensis* superficially resembles *Pyrgillus javanicus* (Mont. & Bosch) Nyl., Mém. Soc. Sci. nat. Cherbourg 5: 334 (1858 [1857]) and related species in Pyrenulaceae (lichenized Ascomycota: Pyrenulales) and is often mistaken for the latter. It can be distinguished from *P. javanicus* by the latter's 3-septate ascospores. The literature on *N. hawaiiensis* contains conflicting reports about the presence of either stictic acid or lichexanthone (Harris, 1990; Tibell, 1996; Mangold et al., 2009); we have only seen material producing stictic acid, not lichexanthone, and the confusion regarding the latter substance might be based on misidentifications of *Pyrgillus javanicus* and allies.

Specimens Examined—**USA**. Florida, Collier County, Fakahatchee Strand Preserve State Park: specimens cited by Lücking et al. (2011). **HAWAII**. The lectotype. **CUBA**. Oriente. Santa Fé, Bro. Hioram 6904, s.n. (NY). **COSTA RICA**. Various localities, specimens cited by Sipman et al. (2012). **NEW CALEDONIA**. The holotype of *Tylophoron dyplotylium*. **AUSTRALIA**. Queensland. Daintree National Park, Mangold 36w (F); various additional localities in eastern Queensland and northeastern New South Wales, specimens cited by Mangold et al. (2009). **FIJI**. Kadavu, Lumbsch 20544b (F). Specimen of *Pyrgillus javanicus* for comparison: **GRENADA**. Parish of St. David, Imshaug 16118 (MSC).

Nadvornikia peninsulae (R. C. Harris) I. Medeiros, Lücking & Lumbsch, comb. nov.

Figure 9A–C

MycoBank #818214

Basionym: *Myriotrema peninsulae* R. C. Harris, Some Florida Lichens: 90. 1990; *Leucodecton peninsulae* (R. C. Harris) Rivas Plata & Lücking in Rivas Plata et al., Lichenologist 42: 184. 2010b. Type: U.S.A. (Florida), Harris 2219 (US!, holotype).

Description—Thallus corticolous, epiperidermal, up to 5-cm diam., continuous; surface smooth to uneven, light yellowish-gray to gray-white; prothallus absent. Thallus in section 150–300 μm thick, cortex loose and irregular, less than 10 μm thick where present, with thick photobiont layer, 150–300 μm thick, interspersed with numerous calcium oxalate crystals (ca. 20- to 30-μm diam.), and indistinct endoperidermal medulla. Photobiont *Trentepohlia*. Ascomata rounded, erumpent to prominent, 0.5- to 1.2-mm diam., 0.3–0.6 mm high; disc more or less covered by 0.1- to 0.6-mm-wide pore, pale gray-brown, white-pruinose; proper margin distinct, fissured, separated from the thalline margin by a narrow split (double margin), forming a prominent, white rim around the

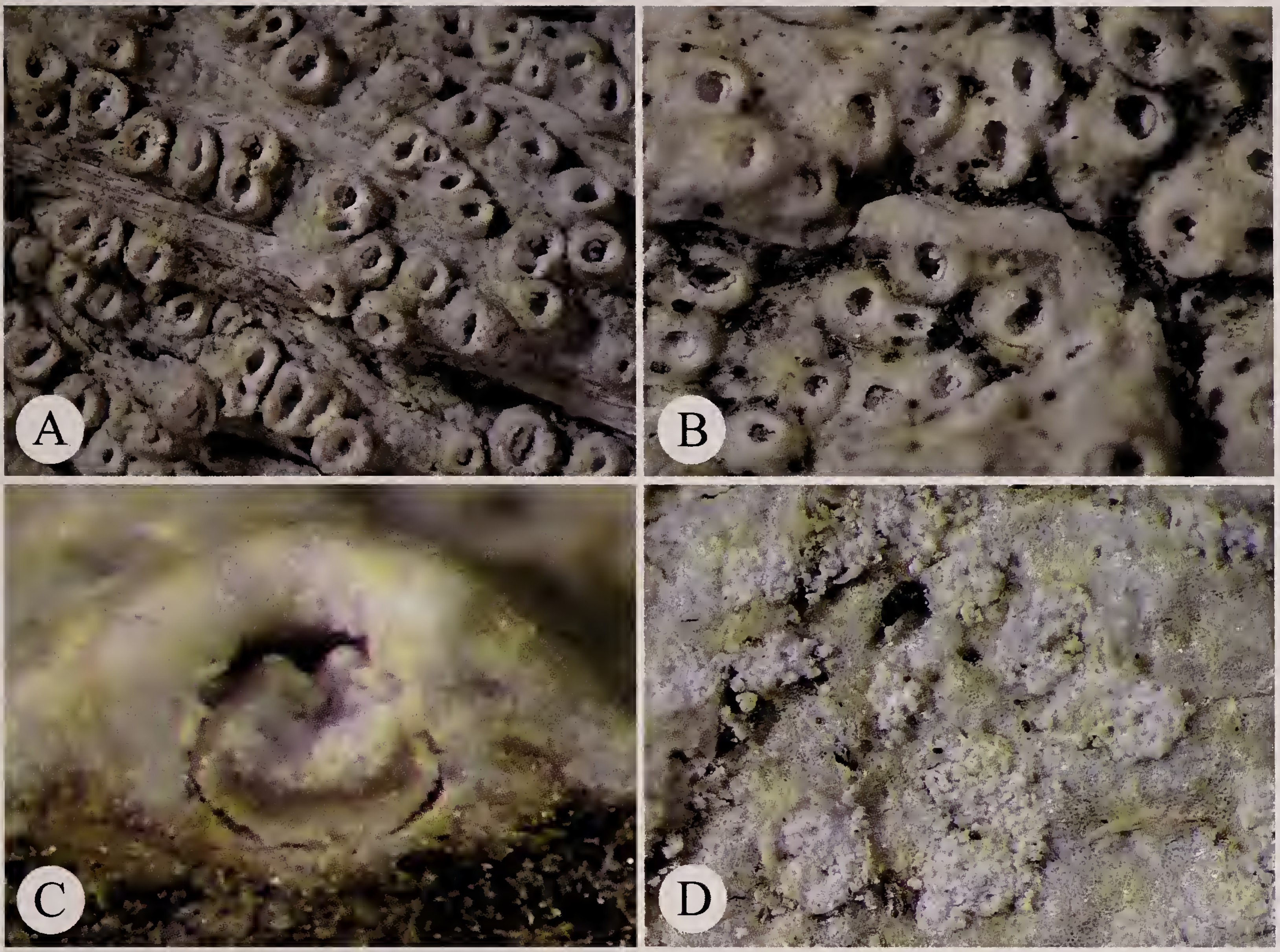

FIG. 9. Morphology and anatomy in Wirthiotremateae. (**A–C**) *Nadvornikia peninsulae* (A: Florida, Lücking 26542; B–C: Florida, Harris 3096A); A–B, thallus with apothecia; C, apothecium in section. (**D**) *N. sorediata* (Florida: Harris 28139), thallus with soralia.

disc; thalline margin thick, entire to eroded, containing layer of wood periderm, concolorous with thallus. Excipulum entire, hyaline to light brown, 10–25 μm wide, prosoplectenchymatous, separated from covering thalline layer by a split; laterally covered by algiferous thallus, 100–250 μm thick; columella absent; hypothecium prosoplectenchymatous, 10–25 μm high, hyaline; hymenium 75–100 μm high, hyaline, clear; epithecium 5–10 μm high, gray and granular. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 55–90 × 10–13 μm. Ascospores 8 per ascus, fusiform, tapering at one end, submuriform with 3–7 transverse and 0–1 longitudinal septa per segment, 16–25 × 5–8 μm, 3–4 times long as wide, hyaline, distoseptate with lens-shaped lumina, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic acid (major) and constictic acid (minor); microscopic section with K+ yellow efflux, not forming red needle-shaped crystals.

ETYMOLOGY—The epithet refers to the type locality in peninsular Florida.

DISTRIBUTION AND ECOLOGY—This species is so far only known from Florida (Harris, 1990, 1995; Lücking et al., 2011) and is likely an endemic species, as it is rather conspicuous but has been found in neither Central America nor in the Caribbean thus far (Sipman et al., 2012; Lücking et al., 2014). It seems to be restricted to rather well-protected pockets of (sub-)tropical humid forest.

DISCUSSION—Like many species now included in Wirthiotremateae, *Nadvornikia peninsulae* has been described by taxonomists as morphologically ambiguous. Harris (1990: 90) states: "*Superficially M. peninsulae looks as if it should be a Thelotrema but I can find no trace of periphysoids.*" This description applies somewhat to several lineages within Wirthiotremateae, particularly *Austrotrema* and the two non-mazaediate species of *Nadvornikia*. Within this tribe, *N. peninsulae* is most similar to *N. expallescens*, but can be easily distinguished by the much larger, prominent apothecia and the larger ascospores. Several species in *Thelotrema* s.s. resemble *M. peninsulae* but, apart from the presence of distinct periphysoids, no species in that genus has a combination of small, submuriform, hyaline ascospores, stictic acid, loosely corticate thallus, and prominent apothecia (Rivas Plata et al., 2010b).

SPECIMENS EXAMINED—**USA**. Florida: The holotype; Florida, Collier County, Fakahatchee Strand Preserve State Park, specimens cited by Lücking et al. (2011).

Nadvornikia sorediata R. C. Harris

Figure 9D

MycoBank #355050

Nadvornikia sorediata R. C. Harris, Some Florida Lichens: 90. 1990. Type: U.S.A. (Florida), Harris 25361 (NY!, holotype).

DESCRIPTION—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, light yellowish-gray; prothallus absent. Thallus in section up to 200 μm thick, ecorticate, with photobiont layer interspersed with calcium oxalate crystals, and endoperidermal medulla. Soralia present, rounded, in raised mounds; soredia irregular, granular, 0.05- to 0.15-mm diam. Photobiont *Trentepohlia*. Ascomata rounded, sessile, 1.0- to 1.6-mm diam., 0.3–0.6 mm high; disc not visible under mazaedial mass, pore 0.5- to 1-mm diam.; proper margin brown, fissured; thalline margin entire to granular-sorediate, white to pale gray. Excipulum entire, hyaline, prosoplectenchymatous; columella absent; hypothecium prosoplectenchymatous hyaline to very pale brown; hymenium hyaline, clear; epithecium not visible due to mazaedial mass. Paraphyses unbranched, apically smooth; periphysoids absent; asci linear to fusiform, 50–100 × 5–8 μm, disintegrating at maturity and releasing ascospores into mazaedial mass. Ascospores 8 per ascus, ellipsoid, 1-septate, 7–10 × 5–6 μm, 1.5 times long as wide, dark olive-brown, appearing black en masse, distoseptate, minutely ornamented, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic (major) and constictic (minor) acids; microscopic section with K+ yellow efflux.

Etymology—The epithet refers to the presence of soredia in this species.

Distribution and Ecology—This species is known from the Neotropics and adjacent subtropical to temperate regions. It is much more restricted geographically than the closely related *Nadvornikia hawaiiensis*. Harris (1990) cites specimens from the United States (Delaware, Florida, Louisiana, and Mississippi), Cuba, and Paraguay, and notes that this species is often found without sexual fruiting bodies. Berger and LaGreca (2014) also report this species from Bermuda. In an ecological study in the Missouri Ozarks, Peck et al. (2004) reported finding it only on the tree base and midbole (i.e., not on downed woody debris or in the canopy). A distribution map is given in Tibell (1996).

Discussion—Although we lack molecular data for this species, its similarity to *Nadvornikia hawaiiensis* in all morphological features except for the presence of soralia leaves no doubt about its taxonomic placement. *Nadvornikia sorediata* is the only sorediate species in the entire tribe, and one of only two species in the tribe (along with *Wirthiotrema santessonii*) with vegetative propagules. Like *N. hawaiiensis*, *N. sorediata* is superficially similar to several unrelated mazaediate species.

Exsiccati—Lichens of Eastern North America Exsiccati, Nos. 114 and 170. See Lendemer (2004) for herbaria to which these have been distributed.

Specimens Examined—**USA**. Florida: The holotype, Harris 26143 (msc). Louisiana: Langlois 1039 (msc).

Wirthiotrema Rivas Plata, Kalb, Frisch & Lumbsch

MycoBank #512786

Wirthiotrema Rivas Plata, Kalb, Frisch & Lumbsch in Rivas Plata et al., Lichenologist 42: 198. 2010a. Type species: *Wirthiotrema glaucopallens* (Nyl.) Rivas Plata & Kalb (≡ *Thelotrema glaucopallens* Nyl.).

Description—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven; prothallus absent. Cortex prosoplectenchymatous and splitting, with irregular to thick photobiont layer interspersed with calcium oxalate crystals, and indistinct endoperidermal medulla. Vegetative propagules absent or present (as pustules/dactyls). Photobiont *Trentepohlia*. Ascomata myriotremoid, rounded, immersed to erumpent; disc concealed by narrow pore; proper margin entire, white to brown, separated or not separated from the thalline margin; thalline margin entire to fissured. Excipulum entire, pale brown to orange-brown, paraplectenchymatous; laterally covered by algiferous thallus; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium hyaline, clear to inspersed; epithecium thin to indistinct. Paraphyses unbranched, apically smooth; periphysoids absent to indistinct; asci clavate. Ascospores 8 per ascus, ellipsoid, muriform, hyaline to brown, I– (non-amyloid). Conidiomata immersed to erumpent when present. Secondary chemistry stictic acid (major) and a variety of associated satellite substances (minor, although constictic acid occasionally major).

Etymology—The generic name *Wirthiotrema* honors the German lichenologist Dr. Volkmar Wirth (born 1943).

Discussion—Two features of this genus distinguish it from all other members of the tribe: the prosoplectenchymatous, internally splitting cortex giving the thallus a very glossy surface and the minute, pore-like often concealed apothecial disc; in some species the apothecia even appear perithecioid. *Wirthiotrema* was described by Rivas Plata et al. (2010a) to accommodate the *Thelotrema glaucopallens* group first recognized by Frisch (2006), a lineage similar to *Leucodecton* but with a peculiar ascospore type that could not be confidently placed in any of the genera newly established by Frisch (2006) and Frisch and Kalb (2006). Molecular data available at the time suggested this group to be unrelated to *Leucodecton*, *Myriotrema*, or *Thelotrema* s.s. (Frisch et al., 2006b), which was confirmed with a much broader taxon sampling (Rivas Plata et al., 2013). *Wirthiotrema* can be distinguished from *Myriotrema* by its non-amyloid ascospores and paraplectenchymatous exciple and by the stictic acid chemistry. It differs from *Leucodecton* by the prosoplectenchymatous, dense, internally splitting cortex, and from *Thelotrema* by its well-developed cortex, pore-like ascomata with usually fused excipulum, and the absence of periphysoids.

Wirthiotrema comprises five species and is found throughout the tropics. According to Rivas Plata et al. (2010a), *Wirthiotrema* is found on bark in lowland and lower montane rainforests in full to partial shade. The distribution and ecology of individual species is addressed in the species descriptions below. A potential species of *Wirthiotrema* possessing norstictic acid (which does not occur elsewhere in the genus or in the entire tribe) was discovered in Costa Rica (Sipman et al., 2012) and provisionally identified as *W.* aff. *glaucopallens*; it has not yet been described due to insufficient material and the lack of molecular data. This species has not been re-studied for this treatment, and its taxonomic placement remains uncertain.

Key to Species—This key includes species of *Wirthiotrema*; similar taxa are mentioned in the species discussions below.

1A. Vegetative propagules (pustules/dactyls) present; apothecia erumpent (but sterile material frequently encountered) .... ***W. santessonii***
1B. Vegetative propagules absent; apothecia immersed ... 2
  2A. Ascospores hyaline 3
    3A. Thalline margin split from proper margin; periphysoids present but indistinct .... ***W. duplomarginatum***
    3B. Thalline margin fused with proper margin; periphysoids absent......... ***W. glaucopallens***

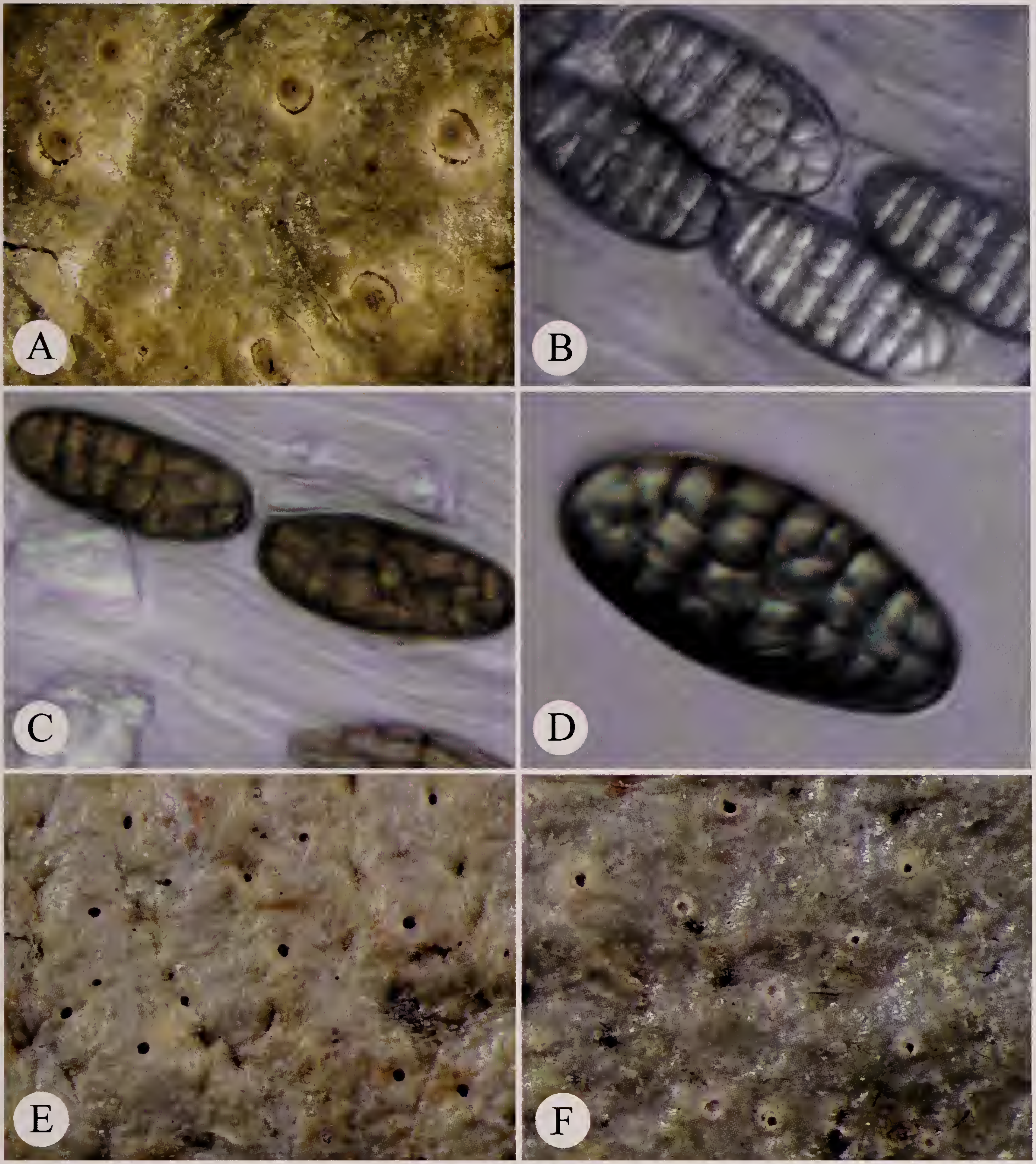

Fig. 10. Morphology and anatomy in Wirthiotremateae. (**A–D**) *Wirthiotrema desquamans* (A, C: lectotype; B: Australia, Mangold s.n.); A, thallus with apothecia; B–D, ascospores. (**E–F**) *W. duplomarginatum* (E: Australia, Lumbsch 19167c; F: Australia, Mangold 34s), thallus with apothecia.

2B. Ascospores brown 4
    4A. Hymenium inspersed .... ***W. trypaneoides***
    4B. Hymenium clear .... ***W. desquamans***

Wirthiotrema desquamans (Müll. Arg.) Lücking

Figure 10A–D

MycoBank #800228

Wirthiotrema desquamans (Müll. Arg.) Lücking in Sipman et al., Phytotaxa 55: 200. 2012; *Anthracothecium desquamans* Müll. Arg., Flora 71: 48. 1888; *Myriotrema desquamans* (Müll. Arg.) Hale, Mycotaxon 11: 133. 1980; *Leptotrema desquamans* (Müll. Arg.) Patw. & Makhija, Bryologist 83: 368. 1980. Type: Australia (Queensland), Berthoud s.n. (G!, lectotype fide Patwardhan & Makhija, 1980: 368).

Thelotrema irosinum Vain., Ann. Acad. Sci. Fenn., Sér. A, 15(6): 174. 1921; *Leptotrema irosinum* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 635. 1923 (1924). Type: Philippines, Elmer 14749 (TUR-VAIN 26766!, lectotype fide Hale, 1981: 278).

Description—Thallus corticolous, epiperidermal, up to 10-cm diam., continuous; surface uneven to verrucose, yellow-green; prothallus absent. Thallus in section 150–300 µm thick, cortex present, dense, 10–30 µm thick, prosoplectenchymatous and splitting, with thick photobiont layer, 100–170(–200) µm thick, interspersed with irregular columns of large calcium oxalate crystals (ca. 25- to 75-µm diam.), and epiperidermal medulla, white, 40–100 µm thick, producing sporadic endoperidermal crystals. Photobiont *Trentepohlia*. Ascomata rounded, perithecioid, immersed to barely erumpent within thalline blisters, 0.1- to 0.4-mm diam., 0.2–0.3 mm high; pore 10–30 µm wide; proper margin indistinct, entire, not split from the thalline margin; thalline margin thick, smooth, green to yellow-green. Excipulum entire, hyaline, 25–50 µm wide, paraplectenchymatous; laterally covered by algiferous thallus, 100–200 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–20 µm high, hyaline; hymenium 150–225 µm high, hyaline, clear; epithecium indistinct. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 150–200 × 15–25 µm. Ascospores 8 per ascus, subglobose, muriform, with 1–3 transverse septa and 1–3 longitudinal septa per segment, 20–35 × 13–18 µm, 1.5–2 times long as wide, brown at maturity, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic acid (major), constictic acid (major to minor), hypoconstictic, cryptostictic, and hypostictic acids (minor to trace).

Illustrations—Mangold et al. (2006). Page 277, figure 1, a–c: Photographs of fertile thallus. Page 279, figure 3, a: Photograph of thallus and ascomata cross section. Page 280, figure 4, a–b: Photographs of ascospores. Mangold et al. (2009). Page 265, figure 64: Photographs of fertile thallus and ascospores (Australian material). Sipman et al. (2012). Page 201, figure 36, A: Photograph of fertile thallus (Costa Rican material).

Etymology—The epithet is derived from the Latin desquamatus, meaning "scaled off," "peeling," or "rubbed bare." It refers to the prosoplectenchymatous splitting (and sometimes flaking) cortex of this species (and other species of *Wirthiotrema*).

Distribution and Ecology—This species has a pantropical distribution (Sipman et al., 2012), although prior to its recent discovery in Costa Rica it was believed to be paleotropical (Mangold et al., 2009). It has been reported from Australia (the type; Mangold et al., 2006, 2009), Costa Rica (Sipman et al., 2012), India (Patwardhan & Makhija, 1980), Papua New Guinea (Aptroot & Sipman, 1991), Malaysia (Sabah; Patwardhan & Kulkarni, 1977), the Philippines (the type of *Thelotrema irosinum*), and Sri Lanka (Hale, 1981; Weerakoon et al., 2010). A distribution map for Australia can be found in Mangold et al. (2006). It is a shady understory rain forest species, often found with species of *Fissurina*, *Myriotrema*, *Ocellularia*, *Rhabdodiscus*, and *Stegobolus*.

Discussion—The perithecioid ascomata and brown ascospores distinguish *Wirthiotrema desquamans* from *W. glaucopallens*, whereas *W. trypaneoides* differs in the inspersed hymenium. *Wirthiotrema desquamans* is very similar in appearance to *Leucodecton compunctum* (Ach.) A. Massal., Atti Inst. Veneto Sci. lett., ed Arti 5(3): 326 (1860), in particular the perithecoid ascomata and dense cortex. However, the latter has longer ascospores and lacks secondary substances (Sipman et al., 2012), and DNA sequence data show that the two species are unrelated (Rivas Plata et al., 2013), providing another striking case of morphological parallelism in Graphidaceae possibly based on shared plesiomorphies (Rivas Plata & Lumbsch, 2011).

Specimens Examined—**AUSTRALIA**. The lectotype; specimens reported as strain I of *Myriotrema desquamans* by Mangold et al. (2009); Mangold 32zb (f), (Queensland, Cape Kimberley) Lumbsch 19166o, 19167c (f). **FIJI**. Viti Levu: Lumbsch 20521i, 20523h, 20526u (f). Kadavu: Lumbsch 20551q (f). **PHILIPPINES**. The lectotype; Rivas Plata & Lücking, 2014 (f).

Wirthiotrema duplomarginatum Lücking, Mangold & Lumbsch

Figure 10E–F

MycoBank #800104

Wirthiotrema duplomarginatum Lücking, Mangold & Lumbsch in Sipman et al., Phytotaxa 55: 202. 2012. Type: Australia (Queensland), Lumbsch & Mangold 19167c (f!, holotype; bri!, isotype).

Description—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, light grayish-olive; prothallus absent. Thallus in section 80–150 µm thick, cortex prosoplectenchymatous and splitting, 10–30 µm thick, with photobiont layer containing calcium oxalate crystals, 60–100 µm thick, and indistinct epi- to endoperidermal medulla. Photobiont *Trentepohlia*. Ascomata erumpent, round, 0.2- to 0.4-mm diam.; disc partially concealed beneath 0.1- to 0.2-mm-wide pore, brown-black, white-pruinose; proper margin distinct, whitish-yellow, entire, separated from the thalline margin by a narrow split (double margin) but usually hidden beneath the pore, forming a pale rim around the disc; thalline margin entire to fissured. Excipulum orange-brown, paraplectenchymatous, separated from covering thalline layer by a split; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium 75–90 µm high, hyaline, clear; epithecium gray-brown and granular. Paraphyses unbranched, apically smooth; periphysoids present but indistinct; asci clavate, 70–90 × 12–17 µm. Ascospores 8 per ascus, ellipsoid, muriform, 5–11 septate transversely and 1–3 septate longitudinally, 20–35 × 7–10 µm, 3–4 times long as wide, hyaline, distoseptate, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic acid (major), α-acetylconstictic and constictic acids (minor), acetylhypoconstictic and cryptostictic acids (minor to trace). Microscopic section with K+ yellow efflux.

Illustrations—Sipman et al. (2012). Page 201, figure 36, B–D: Photographs of fertile thallus and ascospores (Costa Rican material).

Etymology—The epithet refers to the thelotremoid double margin (free excipulum) that distinguishes *Wirthiotrema duplomarginatum* from *W. glaucopallens*, although this feature is difficult to observe as the excipulum is usually hidden within the apothecial pore.

Distribution and Ecology—This species has been reported from Australia (as *Thelotrema myriocarpum*; Mangold et al., 2009) and Costa Rica (Sipman et al., 2012) and hence might have a pantropical distribution. It appears to be a lowland rain forest species adapted to shady conditions.

Discussion—*Wirthiotrema duplomarginatum* is most similar to *W. glaucopallens* (Sipman et al., 2012), from which it is can be distinguished by the presence of indistinct periphysoids and a free excipulum. The two species are also phylogenetically distinct. *Wirthiotrema duplomarginatum* bears some similarity to *Austrotrema myriocarpum* and was identified as that species (as *Thelotrema myriocarpum*) by Mangold et al. (2009). It can be distinguished from the latter by the glossy thallus with completely immersed, small apothecia, and by the smaller ascospores with rounded ends and thin outer walls.

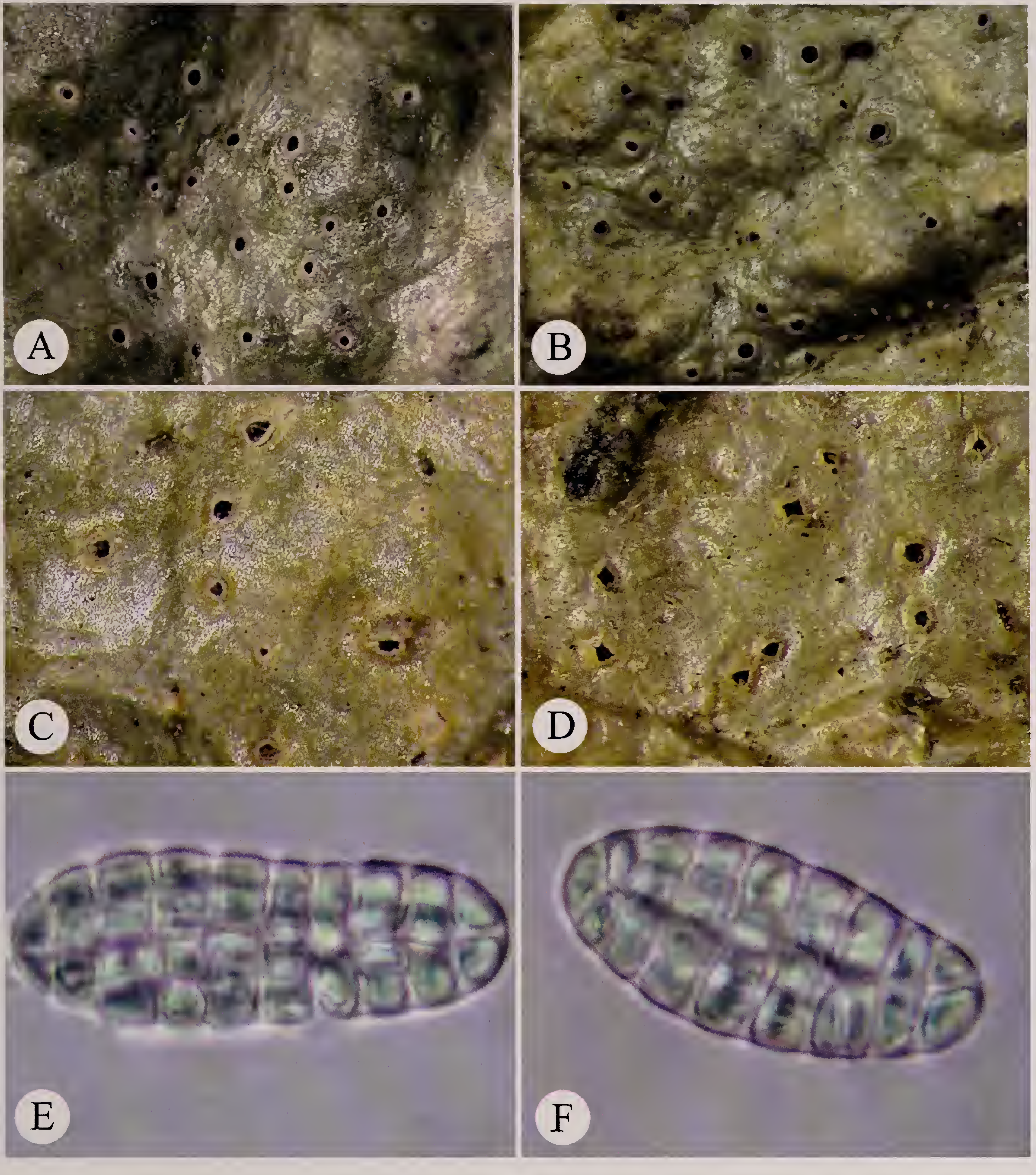

Fig. 11. Morphology and anatomy in Wirthiotremateae. (**A–F**) *Wirthiotrema glaucopallens* (A: Costa Rica, Lücking 21082; B: Brazil, Buck 3080; C–F: lectotype); A–D, thallus with apothecia; E–F, ascospores.

Specimens Examined—**COSTA RICA**. Specimen cited by Sipman et al. (2012). **AUSTRALIA**. Specimen cited by Sipman et al. (2012) and Mangold et al. (2009; as *Thelotrema myriocarpum*).

Wirthiotrema glaucopallens (Nyl.) Rivas Plata & Kalb

Figure 11

MycoBank #512787

Wirthiotrema glaucopallens (Nyl.) Rivas Plata & Kalb in Rivas Plata et al., Lichenologist 42: 201. 2010a; *Thelotrema glaucopallens* Nyl., Ann. Sci. Nat., Bot., Sér. 4, 19: 327. 1863. Type: Cuba, Wright s.n. (fh!, lectotype fide Hale, 1974: 35; h-nyl 22598!, m!, ups!, isolectotypes; Wright, Lich. Cub. 28).

Thelotrema pechuelii Müll. Arg., Linnaea 9: 34. 1880. Type: Congo, Pechuel-Loesche 300 p.p. (g!, holotype).

Thelotrema homopastoides Vain., J. Bot. 34: 207. 1896; *Thelotrema glaucopallens* var. *homopastoides* Vain., Ann. Acad. Sci. Fenn., Ser. A, 6(7): 138. 1915. Type: Lesser Antilles (St. Vincent), Elliott 244 (tur-vain 26845!, lectotype fide Hale, 1974: 35; bm!, isolectotype).

Thelotrema butuanum Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 183. 1921. Type: Philippines, Fénix 28347 p.p. (w!, lectotype fide Hale, 1974: 35; tur-vain 26851!, isolectotype).

Description—Thallus corticolous, epiperidermal, up to 9-cm diam., continuous; surface smooth to uneven, pale yellow-green; prothallus absent. Thallus in section 175–300 μm thick, cortex 15–25 μm thick, with continuous photobiont layer, 125–250 μm thick, thoroughly interspersed with small to moderately large (ca. 10- to 30-μm diam.) calcium oxalate crystals, and irregular medulla, epi- to endoperidermal, 5–75 μm thick, sometimes interspersed with small calcium oxalate crystals. Photobiont *Trentepohlia*. Ascomata rounded, immersed, 0.1- to 0.3-mm diam., 0.1–0.2 mm high; disc partially covered by 0.05- to 0.1-mm-wide pore, gray-brown, white-pruinose; proper margin indistinct, white, entire, not separated from thalline margin; thalline margin thin to thick, smooth, entire, concolorous with thallus. Excipulum entire, pale yellow to orange-brown, 10–20 μm wide, paraplectenchymatous; laterally covered by algiferous thallus, 50–100 μm thick; columella absent; hypothecium prosoplectenchymatous, 10–15 μm high, hyaline; hymenium 65–85 μm high, hyaline, clear; epithecium 5–10 μm high, dark gray-black and granular. Paraphyses unbranched, apically smooth; periphysoids absent; asci clavate, 60–70 × 8–17 μm. Ascospores 8 per ascus, oblong, thickest in distal half, 7–10 transverse septa, 1–3 longitudinal septa, 25–27 × 6–8 μm, 4.5–5.5 times long as wide, hyaline, distoseptate, muriform, I– (not amyloid). Conidiomata not observed. Secondary chemistry stictic acid (major), α-acetylconstictic, constictic and consalazinic acids (minor) and other satellite substances of the stictic acid chemosyndrome (traces); microscopic section with K+ yellow efflux.

Illustrations—Hale (1974). Page 34, figure 16, f–h: Photographs of fertile thalli of *Thelotrema butuanum* (lectotype), *T. homopastoides* (lectotype), and *T. glaucopallens*, respectively. Hale (1978). Page 6, figure 2, i: Photograph of fertile thallus. Frisch (2006). Page 42, plate 3, f: Photograph of fertile thallus. Page 326, plate 17, d: Photograph of fertile thallus. Rivas Plata et al. (2010a). Page 199, figure 1: Photographs of fertile thallus, apothecia, and ascospore. Sipman et al. (2012). Page 201, figure 36, E–F: Photographs of fertile thalli (Costa Rican material). Mercado-Díaz et al. (2015). Page 37, plate 11, G: Photograph of fertile thallus (Puerto Rican material).

Etymology—The epithet refers to the pale sea-green color of the thallus.

Distribution and Ecology—*Wirthiotrema glaucopallens* is a pantropical species, reported from Guatemala, Costa Rica, and Panama (Hale, 1978; Sipman et al., 2012), Cuba, the Lesser Antilles (including Dominica; Hale, 1974), Trinidad and Tobago (Hale, 1978), Guyana and Venezuela (Hale, 1978), the Ivory Coast (Hale, 1978), Ghana, Sierra Leone, and Cameroon (Frisch, 2006), the Congo, South Africa (Hale, 1981), India (Nagarkar et al., 1986), and the Philippines. Notably, it has not yet been collected in Australia (Mangold et al., 2009). According to Hale (1978), it is one of the most frequently encountered lichens at the bases and lower trunks of trees in low-elevation tropical rain forests, and has also been reported from tropical montane forest (Marcano et al., 1996).

Discussion—Molecular phylogenetic data suggested *Wirthiotrema glaucopallens* to be polyphyletic (Rivas Plata et al., 2013), and the new species *W. duplomarginatum* was introduced by Sipman et al. (2012) to account for this topology. Apart from the indistinct periphysoids and the excipulum becoming at least in part free in *W. duplomarginatum*, we found some slight differences in spore size and cortex texture between the two species. The only sequenced specimen of *W. glaucopallens*, from Costa Rica, was compared to the type collection from Cuba and found to agree well with that material.

Papong et al. (2010) synonymized *Myriotrema subanamaliense* Homchantara & Coppins, Lichenologist 34(2): 116 (2002) with *Wirthiotrema glaucopallens*. However, *M. subanamaliense* has amyloid ascospores and hence represents a separate taxon of unresolved generic affinity.

Exsiccati—Lichenes Insulae Cubae, No. 28 (the lectotype and isolectotypes). Lichenotheca Latinoamericana, No. 99. See Sipman (1993) for herbaria to which these have been distributed.

Specimens Examined—**COSTA RICA**. Specimens cited by Sipman et al. (2012). **CUBA**. The lectotype and isolectotypes. **LESSER ANTILLES (ST. VINCENT)**. The lectotype and isolectotype of *Thelotrema homopastoides*. **PHILIPPINES**. The lectotype and isolectotype of *Thelotrema butuanum*.

Wirthiotrema santessonii (Hale) Rivas Plata & Frisch

Figure 12A–C

MycoBank #512788

Wirthiotrema santessonii (Hale) Rivas Plata & Frisch in Rivas Plata et al., Lichenologist 42: 201. 2010a; *Thelotrema santessonii* Hale, Phytologia 26: 417. 1973; *Myriotrema santessonii* (Hale) Hale, Mycotaxon 11: 135. 1980. Type: Ivory Coast, 45 km south of Guiglo, Santesson 10443 (UPS!, holotype; US!, isotype).

Description—Thallus corticolous, epiperidermal, continuous; surface smooth to uneven, grayish-olive, waxy; vegetative propagules present as hollow pustules/dactyls; prothallus absent. Thallus in section up to 200 μm thick, cortex prosoplectenchymatous splitting, up to 12–15(–100) μm thick, with photobiont layer, 60–70 μm thick, containing abundant calcium oxalate crystals, and indistinct medulla, up to 120 μm thick, endoperidrmal. Photobiont *Trentepohlia*. Ascomata erumpent, round, 0.3- to 0.6-mm diam.; disc visible beneath 0.1- to 0.2-mm-wide pore, brown-black, white-pruinose; proper margin entire, brown, not separated from thalline margin; thalline margin entire. Excipulum pale brown, paraplectenchymatous; columella absent; hypothecium prosoplectenchymatous, hyaline; hymenium 100–165 μm high, hyaline, clear; epithecium gray-brown and granular. Paraphyses unbranched, apically smooth; periphysoids absent; asci clavate, 100–130 × 10–18 μm. Ascospores 8 per ascus, ellipsoid, muriform, with 5–9 transverse septa and 1–3 longitudinal septa per segment, 20–24 × 10–13 μm, 1.8–2.3 times long as wide, hyaline, distoseptate, I– (non-amyloid). Conidiomata pycnidia, low to immersed, 0.4- to 0.5-mm diam., conidia 2.5–3.2 × 1–1.2 μm. Secondary chemistry stictic acid (major), α-acetylconstictic, consalazinic, and constictic acids (minor); microscopic section with K+ yellow efflux.

Illustrations—Frisch (2006). Page 334, figure 107: Drawing of ascospores and ascomata cross section. Page 326, plate 17, e–f: Photographs of fertile thalli. Rivas Plata et al. (2010a). Page 200, figure 2, D–F: Photographs of fertile thallus, apothecia, and pustules.

Etymology—This species was named in honor of the Swedish lichenologist Rolf Santesson (1916–2013).

Distribution and Ecology—This paleotropical species is known from tropical Africa (Ivory Coast, Cameroon, and Tanzania; Frisch, 2006), Sri Lanka (Hale, 1981), New Caledonia (Hale, 1981), and Hawaii (Hale, 1981) and Singapore (Sipman, 2010). It has similar habitat preferences as *Wirthiotrema glaucopallens*, growing at tree and liana bases in lowland rainforest; however, in contrast with *W. glaucopallens*, *W. santessonii* was not found in mangroves by Frisch (2006).

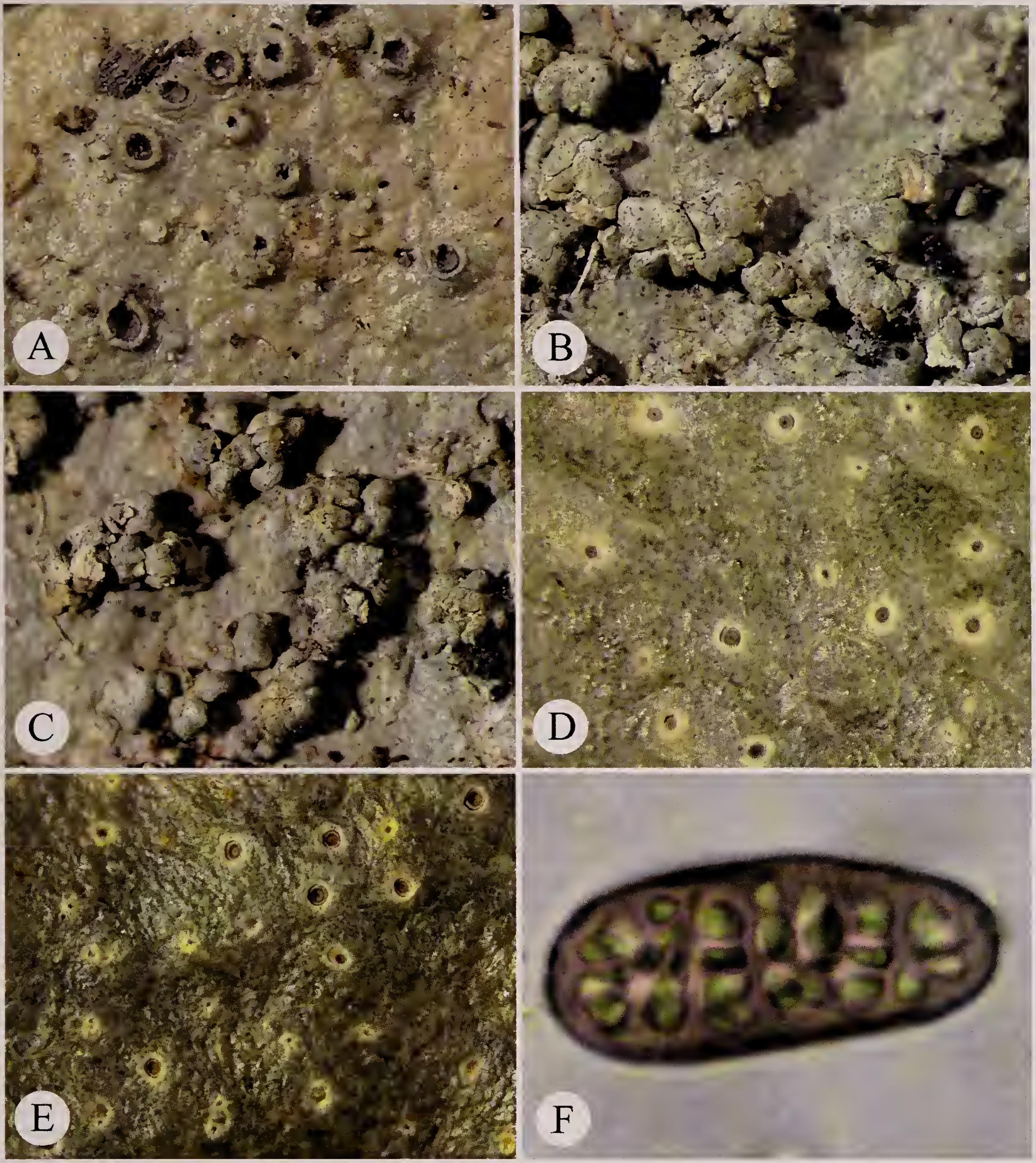

Fig. 12. Morphology and anatomy in Wirthiotremateae. (**A–C**) *Wirthiotrema santessonii* (holotype); A, thallus with apothecia; B–C, thallus with dactyls. (**D–F**) *W. trypaneoides* (D, F: Australia, Lumbsch 19167v; E: Australia, Elix 20202); D–E, thallus with apothecia; F, ascospore.

Discussion—This is one of only two species in the Wirthiotremateae that produce vegetative propagules. The other (*Nadvornikia sorediata*) forms soredia, while *W. santessonii* produces corticate pustules/dactyls. Sterile material of this species has been frequently collected (Frisch, 2006). The pustules/dactyls of *W. santessonii* may be involved in gas exchange as well as dispersal (Frisch, 2006). According to Rivas Plata et al. (2010a), these structures are highly variable in terms of size and coarseness, and often break open at the apex to expose a central cavity. *Wirthiotrema santessonii* can be distinguished from other *Wirthiotrema* species by these propagules and also by the distinctly erumpent apothecia; otherwise, it is most similar to *W. glaucopallens* (Frisch, 2006; Rivas Plata et al., 2010a).

Specimens Examined—**IVORY COAST**. The holotype and isotype.

Wirthiotrema trypaneoides (Nyl.) Rivas Plata & Lücking

Figure 12D–F

MycoBank #512789

Wirthiotrema trypaneoides (Nyl.) Rivas Plata & Lücking in Rivas Plata et al., Lichenologist 42: 201. 2010a; *Thelotrema trypaneoides* Nyl., Ann. Sci. Nat., Bot., Sér. 4, 19: 335. 1863; *Leptotrema trypa-*

neoides (Nyl.) Riddle, Bull. Torrey Bot. Club 43: 151. 1916; *Myriotrema trypaneoides* (Nyl.) Hale, Mycotaxon 11: 135. 1980. Type: Cuba, Wright 156 (FH-TUCK!, lectotype fide Hale, 1978: 54; BRU!, UPS, US!, isolectotypes).

Thelotrema subterebrans Nyl., Flora 59: 561. 1876; *Leptotrema subterebrans* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 640. 1923 (1924). Type: Cuba, Wright 520 (H-NYL 22514!, lectotype fide Hale, 1978: 55).

Thelotrema laevius Vain., J. Bot. 34: 207. 1896; *Leptotrema laevius* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 635. 1923 (1924). Type: Lesser Antilles (St. Vincent), Elliott s.n. (TUR-VAIN 26774!, holotype).

Description—Thallus corticolous, epiperidermal, up to 6-cm diam., continuous; surface smooth to uneven, grayish-green; prothallus absent. Thallus in section 125–250 μm thick, cortex present, 5–15 μm thick, prosoplectenchymatous and splitting, with continuous photobiont layer, 110–240 μm thick, interspersed with many irregular calcium oxalate crystals (ca. 25-μm diam.), and indistinct endoperidermal medulla. Photobiont *Trentepohlia*. Ascomata rounded, immersed to barely erumpent, 0.1- to 0.5-mm diam., 0.2–0.3 mm high; disc partially covered by 0.05- to 0.1-mm-wide pore, flesh-colored to gray-brown; proper margin white, entire, not separated from the thalline margin; thalline margin thick, smooth, concolorous with thallus. Excipulum entire, pale yellow-brown to brown, 15–20 μm wide (thickest apically), paraplectenchymatous, upper surface with small gray crystals; laterally covered by algiferous thallus, 50–100 μm thick; columella absent; hypothecium prosoplectenchymatous, 12–25 μm high, hyaline to very pale brown; hymenium 150–200 μm high, hyaline, inspersed with oil droplets; epithecium 5–10 μm high, gray-brown and granular. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 120–180 × 10–20 μm. Ascospores 8 per ascus, ellipsoid, muriform with 7–11 transverse septa and 1–5 longitudinal septa per segment, 25–40 × 8–15 μm, 2.5–3.5 times long as wide, brown at maturity, I– (non-amyloid). Conidiomata not observed. Secondary chemistry stictic and constictic acids (major), cryptostictic, hypoconstictic, and hypostictic acids (minor and trace); microscopic section with K+ yellow efflux.

Illustrations—Hale (1978). Page 6, figure 2, a: Photograph of fertile thallus (lectotype). Page 51, figure 14, l: Photograph of fertile thallus. Mangold et al. (2006). Page 278, figure 2, d–f: Photographs of fertile thallus. Page 279, figure 3, d: Photograph of thallus and ascomata cross section. Page 280, figure 4, i: Photograph of ascospore. Rivas Plata et al. (2010a). Page 200, figure 2, A–C: Photographs of fertile thallus, apothecia, and ascospore. Sipman et al. (2012). Page 201, figure 36, H: Photograph of fertile thallus (Costa Rican material).

Etymology—The epithet is presumably derived from the Greek trypanon ("to bore") because the apothecial openings resemble minute auger holes.

Distribution and Ecology—Hale (1978) wrote that in Panama this species was uncommon, and most often collected at the bases of trees and saplings. *Wirthiotrema trypaneoides* has a pantropical distribution and is found in lowland rain forests (Mangold et al., 2009). It has been reported from Australia (Mangold et al., 2006), Bermuda (Riddle, 1916), Costa Rica (Sipman et al., 2012), Cuba (the type; the type of *Thelotrema subterebrans*), India (Patwardhan & Kulkarni, 1977), Panama (Hale, 1978), and Saint Vincent and the Grenadines (the type of *Thelotrema laevius*). A distribution map for Australia can be found in Mangold et al. (2006).

Discussion—*Wirthiotrema trypaneoides* can be distinguished from the other species of *Wirthiotrema* with brown ascospores, *W. desquamans*, by its inspersed hymenium. The superficially similar *Thelotrema defectum* Hale lacks stictic acid and a cortex, and similar species of *Leucodecton* have a more loosely organized cortex.

Exsiccati—Lichenes Insulae Cubae, Nos. 156 (the lectotype and isolectotypes) and 520 (the lectotype of *Thelotrema subterebrans*).

Specimens Examined—**CUBA**. The lectotype and isolectotype; the lectotype of *Thelotrema subterebrans*. **LESSER ANTILLES (ST. VINCENT)**. The holotype of *Thelotrema laevius*. **COSTA RICA**. Specimens cited by Sipman et al. (2012). **VENEZUELA**: Lücking 32003 (F, VEN).

Acknowledgments

We thank the curators of herbaria cited in this paper for providing access to specimens. Molecular work was performed in the Pritzker Laboratory for Molecular Systematics and Evolution at the Field Museum; the first author thanks Kevin Feldheim and Steve Leavitt for their instruction and assistance with molecular techniques and Luis Allende and Marissa Locke for their camaraderie in the lab. This research was supported by two National Science Foundation grants to the Field Museum: DBI-1156594, REU Site: Access to Global Biodiversity Studies for Undergraduates (PI: Petra Sierwald, Co-PI: Kenneth Angielczyk) and DEB-1025861, ATM–Assembling a taxonomic monograph: The lichen family Graphidaceae (PI: Thorsten Lumbsch, Co-PI: Robert Lücking). We thank the two anonymous reviewers for their comments which substantially improved the manuscript.

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